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The Journal of the North Carolina
State Museum of Natural Sciences

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number 18

june 1993

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CODN BRIMD 7

ISSN 0193-4406

The Myriapod Types of Oscar Harger (Arthropoda: Diplopoda, Chilopoda)

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ABSTRACT—The type specimens of all five milliped species—*Trichopetalum lunatum*, *T. glomeratum*, *T. iuloides*, *Iulus furcifer*, and *Polydesmus armatus*—and one of the two centipedes, *Lithobius pinetorum*, authored by Oscar Harger in his only paper on myriapods and previously thought to be lost, are housed at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut. From our knowledge of the itinerary of the Yale paleontological expedition of 1871, we know the type locality of *T. glomeratum*, *I. furcifer*, *P. armatus*, and *L. pinetorum*, previously stated as the “John Day River Valley, Oregon” is restricted to the vicinity of Canyon City, Grant County, on the western slope of the Blue Mountains. The female holotype confirms that *T. glomeratum* is a representative of the chordeumatoid family Conotylidae, and the name is assigned provisionally to *Taiyutyla* pending collection of a male topotype. Unidentifiable female conotylids are also reported from another area in eastern Oregon and the Snake Mountains in eastern Nevada, which suggests that the family is widespread in montane forests at high elevations in the generally arid Columbia Plateau and Basin and Range Physiographic Provinces. To facilitate future studies, I provide gonopod drawings of male syntypes for *I. furcifer* and *P. armatus*.

One of the more obscure authors of North American myriapods is Oscar Harger (1843–87), whose sole publication on these arthropods (Harger 1872) described the milliped genus *Trichopetalum* and seven species, two centipedes (*Lithobius pinetorum* and *Geophilus gracilis*) and five millipeds (*Trichopetalum lunatum*, *T. glomeratum*, *T. iuloides*, *Iulus furcifer*, and *Polydesmus armatus*).

Born at Oxford, Connecticut, Harger attended the Connecticut Literary Institute at Suffield and Yale College, graduating from the latter with honors in 1868 (Schuchert and LeVene 1940). After briefly studying zoology under Professor A. E. Verrill, Harger became the first assistant to the vertebrate paleontologist, O. C. Marsh, participating on the latter's expeditions into the American West in 1871 and 1873. From July to September 1872, Harger dredged marine organisms on a Coast Survey steamer with Professors Verrill and Sydney I. Smith, Yale's first professor of Comparative Anatomy, who earlier had been naturalist to the U.S. Lake Survey and collected the types

of *T. iuloides*. Harger was studious and an active reader, and Marsh valued his scientific opinions in paleontology. However, Marsh would not allow Harger to publish on vertebrate fossils, either alone or jointly with him, so Harger's only papers are on invertebrates—that of 1872 on myriapods, two on isopods, and one on a fossil spider.

From 1870 to 1873, Marsh led four vertebrate paleontological expeditions of Yale students and recent graduates into the West (Schuchert and LeVene 1940). The idea of such efforts arose from preliminary explorations he made on a trip to the end of the trans-continental railroad in Wyoming in August 1868 after attending a scientific meeting in Chicago. The 1871 expedition traveled to regions of Kansas, Wyoming, and Utah, where Harger collected 10 fossil species. The group then rested a few days in Salt Lake City with Brigham Young while Marsh prepared to explore a new area, the John Day River Basin in central Oregon. After traveling 12 days by rail and stage, the party crossed the Blue Mountains and arrived at Canyon City, Oregon, on the John Day River on 17 October 1871, where it waited several days for a military escort from Fort Harney, 75 mi (120 km) to the south. The group collected fossils from 31 October to 8 November in the John Day region before traveling down the Columbia River to Portland; it then traveled to San Francisco and returned east directly by rail or by boat via Panama.

While the expedition was in the John Day River area, Harger, or Harger and Professor G. H. Collier, collected four Oregon myriapods that he described in 1872—*L. pinetorum*, *T. glomeratum*, *I. furcifer*, and *P. armatus*. Both the publication and labels in the vials give the locality as just the "John Day River Valley," but knowledge of the group's activities enabled me to infer a more precise site. The John Day River arises on the western slope of the Blue Mountains in Grant and Umatilla counties, flows westward into Wheeler County, then heads northward to the Columbia River forming the boundaries between Wheeler/Wasco and Sherman/Gilliam counties. It is not to be confused with Days Creek, Douglas County, in the Umpqua River drainage of southwestern Oregon, the probable type locality for *Zantona douglasia* Chamberlin and *Bollmanella oregona* Chamberlin (Shear 1974, Gardner and Shelley 1989), which Chamberlin (1941a) misnamed as "John Day Creek." Because most millipeds require moist leaf litter and much of the John Day Basin is in the arid rain shadow of the Cascade Mountains, I (Shelley 1990) speculated that the site was probably near the confluence of the John Day and Columbia rivers in either Sherman or Gilliam county. However, as all the myriapods were collected in October 1871, and the expedition reached Canyon City on 17 October and only collected fossils from 31 October to 8 November

after waiting for the military escort, it is evident that during most of the part of October that the group was in the John Day Valley, it was resting in Canyon City. Consequently, there was ample time for relaxed explorations in the vicinity of Canyon City, and I, therefore, believe that Harger's myriapods were collected near this town. Because Harger's paper specifies that *L. pinetorum*, *I. furcifer*, and *P. armatus* were collected by Professor Collier and himself, and *T. glomeratum* was taken by Harger alone, collecting probably occurred on at least two different dates, as one day Harger went out alone and the other he was accompanied by Collier. There could be as few as one site and as many as four, but further specification is not possible with what we know now. Consequently, the type locality for all of Harger's Oregon species is restricted to the vicinity of Canyon City, Grant County, on the western slope of the Blue Mountains.

Harger's centipedes have received little attention since their description. They were included in the catalog of North American myriapods by Bollman (1893), who noted that *G. gracilis* Harger, 1872, was preoccupied by *G. gracilis* Meinert, 1870, proposed for a European geophilomorph. Cook and Collins (1891) remarked that Harger's description of *G. gracilis* conformed very closely to *Schendyla nemorensis* (C. L. Koch, 1837), and the former is now regarded as a junior synonym (Crabill 1953, 1961). Stuxberg (1875) included *L. pinetorum* in his list of North American lithobiids, but he had no personal knowledge of the species. Kevan (1983a) listed both species as potential inhabitants of Canada, recognizing the synonymy of *G. gracilis* under *S. nemorensis*.

In contrast to the centipeds, Harger's millipeds have been cited in a number of publications, but the type specimens were thought to be lost. Chamberlin and Hoffman (1958) stated that their "present location [was] unknown" or that they were "not known to exist," and similarly, Shear (1971, 1972) said that the holotypes of *T. glomeratum* and *T. iuloides* were lost and that the whereabouts of that of *T. lunatum* was unknown. Causey (1967) guessed right when she stated that the holotype of *T. lunatum* was at the "Peabody Museum of Natural History, Yale University, if extant," but evidently she made no inquiries to confirm this supposition. While recently visiting the Peabody's Museum's collection, I unexpectedly discovered these types in the myriapod cabinet, where they have languished in obscurity for 120 years. A few vials were still capped with wax and had not been touched for decades. The types of *P. armatus* were in the general collection and not labeled as such, but those of the other millipeds were clearly marked as types and grouped in a clamp-top jar. A concerted search failed to reveal the types of *G. gracilis*, which ap-

parently are lost, but those of *L. pinetorum* were in an individual vial and clearly labeled. The sample consists of 12 nearly legless syntypes, seven males and five females, and is number 2175; according to the label it was collected by Harger alone, whereas the published account states that it was collected by him and Professor Collier.

All the millipeds are listed in the continental checklist (Chamberlin and Hoffman 1958), and detailed accounts of those Harger assigned to *Trichopetalum* have recently appeared (Palmen 1952; Shear 1971, 1982; Shelley 1988, In Press).

In the following accounts I update these reports by providing information on the type specimens, a brief historical review of each species, and pertinent anatomical observations. Complete synonymies are presented, and each species is placed in its proper order and family.

Chordeumatida: Trichopetalidae

Trichopetalum lunatum Harger

Trichopetalum lunatum Harger, 1872:3, pl. II, figs. 1–4. Ryder, 1881:527. Packard, 1883:192. McNeill, 1888:8. Cook and Collins, 1895:63–64, pl. III, figs. 52–54. Williams and Hefner, 1928:115, fig. 12d. Causey, 1951:119, figs. 6–8; 1967:80, fig. 1. Palmen, 1952:8–11, figs. 10–17. Chamberlin and Hoffman, 1958:102–103. Shear, 1972:277, figs. 497–499. Kevan, 1983b:2967. Shelley, 1988:1650.

Trichopetalum album Cook and Collins, 1895:64–66, pls. II–III, figs. 22–29, 36–45. Chamberlin and Hoffman, 1958:102.

Type Specimens—Five male and nine female syntypes (nos. 2208–2209) collected by O. Harger in May 1872 at New Haven, New Haven County, Connecticut; one male and one female syntype (no. 2125) taken by an unknown collector on an unknown date at Mt. Carmel, ca. 7 mi (11.2 km) north of New Haven, New Haven County.

Remarks—Harger assigned three new species to his genus *Trichopetalum* but did not specify the type species, so Cook and Collins (1895) subsequently designated *T. lunatum*. It is the only one of Harger's five milliped species to retain its original combination. The identity of *T. lunatum* has been well established by Cook and Collins (1895), Palmen (1952), Causey (1967), and Shear (1972); a male syntype from New Haven that I dissected conformed to these

accounts. For details of the genitalia, refer to the illustrations in Palmen (1952) and Shear (1972).

Chordeumatida: Conotylidae

Taiyutyla glomerata (Harger), new combination

Trichopetalum glomeratum Harger, 1872:118, pl. II, fig. 5. Ryder, 1881:527. Packard, 1883:192. McNeill, 1888:8. Chamberlin and Hoffman, 1958:105. Shear, 1971:63.

Craspedosoma glomeratum: Bollman, 1893:120.

Conotyla glomerata: Cook and Collins, 1895:78. Cook, 1904:69.

Type Specimen—Female holotype (No. 2173) collected by O. Harger in October 1871 from the vicinity of Canyon City, in the John Day River Valley, Grant County, Oregon.

Remarks—The holotype is somewhat deformed, and its genitalia have been dissected and are lost.

Cook and Collins (1895) stated that the original description was too brief to allow accurate generic placement but that the segment number, short fifth antennomere, and triangular eye patch resembled the condition in *Conotyla*. Shear (1971) agreed that accurate generic placement was impossible but perceived a similarity to *Taiyutyla*; he did not think the name could be referred to either *Trichopetalum* or *Conotyla* and considered it a *nomen dubium*. The holotype is about 8 mm long and has 30 post cephalic segments with obvious lateral tergal knobs that give rise to two prominent setae, so it is clearly a conotylid. Generic placement is impossible to determine with certainty until a male topotype is obtained, but the milliped is smaller and its lateral setae are much longer than those of comparative specimens of *Conotyla atrolineata* (Bollman), the western-most known representative of this genus, occurring in central British Columbia, northeastern Washington, and northern Idaho, over 200 mi (320 km) north northeast of Canyon City. These considerations tend to exclude *Conotyla*, but the type locality is also well removed from most of the known distributions of the other northwestern conotylid genera *Bollmanella* and *Taiyutyla*, which are from southern coastal Oregon to Mason County, Washington, and in the Coast Ranges from San Francisco Bay to the Columbia River, respectively (Shear 1974, 1986). However, one species in each of these genera occurs east of the above ranges, *B. bifurcata* Shear, in the Wallowa Mountains, Wallowa County, Oregon, and *T. curvata* Loomis and Schmitt, in Lincoln County, Montana, so either genus could occur in the Blue Mountains, which occupy an intermediate

geographical position between the Coast Range and both the Wallowa Mountains and Montana. Furthermore, Canyon City is only about 110 mi (176 km) southwest of the type locality of *B. bifurcata*. Therefore, I borrowed the types of both *B. bifurcata* and *T. curvata* for direct comparisons with that of *glomerata*. Few setae remain on the types of *B. bifurcata*, and those that do exist, on the caudal end of the male holotype, seem shorter and are not nearly as prominent as are those on *glomerata*. However, the setae on *glomerata* agree closely in length and prominence with those on the holotype of *T. curvata*. There is reasonable agreement in body dimensions between *glomerata* and both other conotylids, but because of the similarity in the setae, I provisionally assign *glomerata* to *Taiyutyla*, pending collection of a male topotype. This change, which formalizes Shear's (1971) perception of similarity to *Taiyutyla*, also necessitates the feminine suffix of the specific name. Fieldwork is needed in the Blue Mountains to collect a male conotylid to determine the identity and generic position of *glomerata* and to confirm or disprove this decision.

Present evidence shows that the Conotylidae is much more widespread in the West than currently known. There is a female in the Florida State Collection of Arthropods from 12.5 mi (20 km) south of Baker City, Baker County, Oregon, that might be conspecific with *glomerata*, although this site is east of the Blue Mountains and presumably is drier than Canyon City. I also recently received two female conotylids that are superficially very similar to *glomerata* from the Snake Mountains, White Pine County, Nevada, in the eastern part of that state and hundreds of kilometers from any known site for the family. These two records plus *glomerata* suggest that conotylids could be scattered across the arid Columbia Plateau and Basin and Range Physiographic Provinces, where they are undoubtedly restricted to cooler, forested regions at high elevations. The Ruby Mountains near Elko, Nevada, is another plausible area for conotylids, as are ranges in the central part of that state. Because only a few millipeds of any family have ever been collected from the "inselberg" mountains of these provinces, a concerted field effort is needed to both clarify the systematic positions of these conotylids and document the total diplopod fauna.

Chordeumatida: Caseyidae

Underwoodia iuloides (Harger)

Trichopetalum iuloides Harger, 1872:118. pl II, fig. 6.

Trichopetalum juloides: Ryder, 1881:527.

Trichopetalum iuloides: Packard, 1883:192.

Trichopetalum iuloides: McNeill, 1888:8.

Chordeuma iuloides: Bollman, 1893:121.

Underwoodia polygama Cook and Collins, 1895:80–82, pl. X, figs. 180–190. Paleman, 1952:2–8, figs. 1–9a. Chamberlin and Hoffman, 1958:107. Kevan, 1983b:2968.

Underwoodia iuloides: Cook and Collins, 1895:83–84, pl. X, figs. 177–178. Chamberlin and Hoffman, 1958:107. Kevan, 1983b:2968. Shelley, 1988:1648–1649; In Press:

Type Specimens—Eight female syntypes (No. 2207) collected by S. I. Smith in 1871 at Simon's Harbor (misspelled as Simmon's) on the north shore of Lake Superior, Ontario, Canada. This site is now in Pukaskwa National Park.

Remarks—A review of *Underwoodia* with a description, discussion, and illustrations of *U. iuloides* is in press. For details on this species, see Shelley (1988).

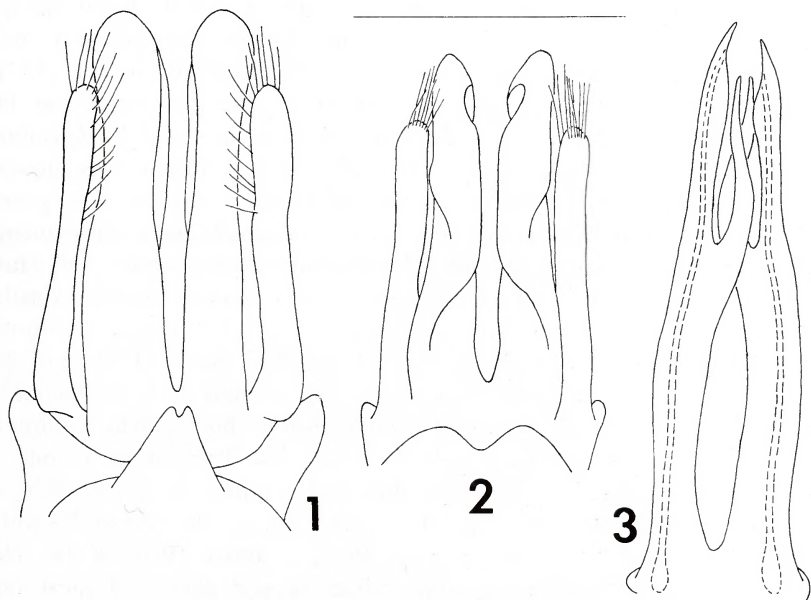


Fig. 1–3. *Bollmaniulus furcifer*, male syntype. 1, anterior gonopods, anterior view. 2, the same, posterior view. 3, posterior gonopods, anterior view. Scale line = 2.2 mm for figs. 1–2, 1.6 mm for fig. 3.

Julida: Parajulidae
Bollmaniulus furcifer (Harger)

Figs. 1–3

Iulus furcifer Harger, 1872:119, pl. II, fig. 7.

Parajulus furcifer: Bollman, 1887:44. Cook, 1904:70–71, pl. V, figs. 5a–e. Chamberlin, 1920:35.

Paraiulus furcifer: Brolemann, 1895:69, pl. 7, figs. 21–23.

Bollmaniulus furcifer: Verhoeff, 1926:65. Chamberlin and Hoffman, 1958:133. Buckett, 1964:18. Kevin, 1983b:2964.

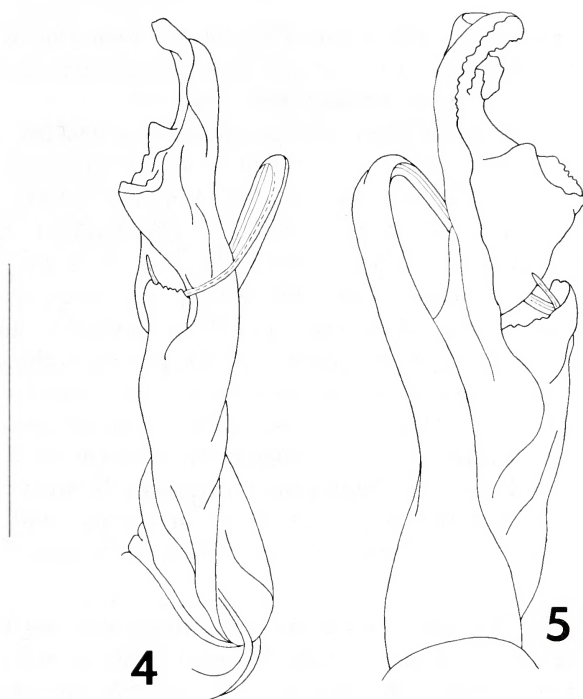
Taijulus furcifer: Chamberlin, 1938:205.

Caliulus furcifer: Chamberlin, 1940:15; 1944:80.

Type Specimens—Three male and 13 female syntypes (No. 2172), most highly fragmented, collected by O. Harger and G. H. Collier in October 1871 from the vicinity of Canyon City, in the John Day River Valley, Grant County, Oregon.

Remarks—Bollman (1887) transferred this species into *Parajulus*, misspelled as *Paraiulus* by Brolemann (1895), and Cook (1904) recorded it from Corvallis, Oregon. Chamberlin (1920) reported it from Claremont, Los Angeles County, California, surely a misidentification of another, possible congeneric parajulid. Verhoeff (1926) listed *furcifer* as the only component of his new genus *Bollmaniulus*, thereby making it the type species by monotypy as reported by Jeekel (1971). He did not specifically designate *furcifer* as the generotype, so this status does not result from original designation, as stated by Chamberlin and Hoffman (1958). Chamberlin (1938, 1940) evidently was unaware of Verhoeff's action when he transferred *furcifer* into his new genera *Taijulus* and *Caliulus*, respectively, both of which have subsequently been placed in synonymy under *Bollmaniulus* (Chamberlin and Hoffman 1958, Hoffman 1979). Chamberlin (1944) repeated the combination *C. furcifer* for a form from McCloud, Siskiyou County, California, and added that the species was common over much of Oregon and California. Buckett (1964) recognized the combination *Bollmaniulus furcifer* and stated that it ranged from British Columbia into California.

As noted by Hoffman (1979, 1992), the Parajulidae is one of the two most dominant Nearctic diplopod families in terms of component genera and species, the other being the Xystodesmidae (Polydesmida). It was studied from 1948 to about 1974 by Dr. Nell B. Causey, who amassed a large collection and examined most type specimens while conducting a detailed family revision. Unfortunately, she never completed the project and published only a few brief papers before her death in 1979. Consequently, knowledge of the Parajulidae is not nearly as advanced as those of the other major Nearctic diplopod families. Work on the taxon must essentially begin anew, a daunting task because of the diversity of the family and the enormous amount of preserved material in nearly every major and minor milliped repository on the continent. The types of *I. furcifer* will be crucial to an investigation of Pacific parajulids, because as the eighth oldest generic name in the family, *Bollmaniulus* has priority over such other nominal Pacific



Figs. 4–5 *Chonaphe armata*, male syntype. 4, telopodite of left gonopod, medial view. 5, the same, lateral view. Scale line = 1.14 mm for fig. 4, 1.0 mm for fig. 5.

genera as *Saiulus*, *Spathiulus*, *Sophiulus*, *Codiulus*, and *Simiulus*, all authored by Chamberlin (1940), *Tuniulus* (Chamberlin 1941b), and *Mulaikiulus* (Chamberlin 1941a), so additional generic synonymies could result from a study of these western forms. For the benefit of future students, I have included drawings of the gonopods of a male syntype (Figs.1–3).

Polydesmida: Xystodesmidae

Chonaphe armata (Harger)

Fig. 4–5

Polydesmus armatus Harger, 1872:119–120, pl. II, fig. 8.

Leptodesmus armatus: Bollman, 1893:122. Chamberlin, 1911:264.

Chonaphe armata: Cook, 1904:56–57, pl. III, figs. 2a–c. Attems, 1931:65–67, figs. 100–101; 1938:156, fig. 177. Chamberlin, 1949:125. Chamberlin and Hoffman, 1958:27. Kevan, 1983b:2968. Shelley, 1990:2314.

Type Specimens—One male and two female syntypes, all highly fragmented, collected by O. Harger and G. H. Collier in October

1871 from the vicinity of Canyon City, in the John Day River Valley, Grant County Oregon. This sample was discovered in the general milliped collection and is unnumbered.

Remarks—Harger's single gonopod illustration enabled Cook (1904) to recognize that a male sent to him from an unknown locality in Washington was referable to *armatus*. Bollman (1893) had earlier transferred *armatus* to *Leptodesmus*, a combination repeated by Chamberlin (1911), but Cook (1904) assigned it to his new genus, *Chonaphe*, a combination that subsequently has been recognized by Attems (1931, 1938), Chamberlin (1949), Chamberlin and Hoffman (1958), and Shelley (1990). Cook (1904) provided three additional genitalia drawings, and I include here medial and lateral views of the gonopod of a male syntype (Figs. 4–5). Five nominal species comprise *Chonaphe*, but Hoffman (1979) thought these might be subspecies. I (Shelley 1990) found few significant differences between these forms and concluded that the genus might be monotypic with *C. armata* being the oldest name. I am preparing a generic revision.

ACKNOWLEDGMENTS—I thank C. L. Remington and R. J. Papedis for providing access to the Peabody Museum holdings and subsequently loaning Harger's types. The holotype of *Taiyutyla curvata*, housed at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., was loaned by J. A. Coddington; the types of *Bollmanella bifurcata*, housed at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, were loaned by H. W. Levi. The conotyloid from Baker County, Oregon, was discovered in material loaned by G. B. Edwards, Florida State Collection of Arthropods, Gainesville. Cathy Wood typed and retyped numerous drafts of the manuscript, and figures 1–5 were prepared by R. G. Kuhler.

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Accepted 9 September 1992

THE SEASIDE SPARROW, ITS BIOLOGY AND MANAGEMENT

Edited by

Thomas L. Quay, John B. Funderburg, Jr., David S. Lee,
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The proceedings of a symposium held at Raleigh, North Carolina, in October 1981, this book presents the keynote address of F. Eugene Hester, Deputy Director of the U.S. Fish and Wildlife Service, a bibliography of publications on the Seaside Sparrow, and 16 major papers on the species. Authors include Arthur W. Cooper, Oliver L. Austin, Jr., Herbert W. Kale, II, William Post, Harold W. Werner, Glen E. Woolfenden, Mary Victoria McDonald, Jon S. Greenlaw, Michael F. Delany, James A. Mosher, Thomas L. Merriam, James A. Kushlan, Oron L. Bass, Jr., Dale L. Taylor, Thomas A. Webber, and George F. Gee. A full-color frontispiece by John Henry Dick illustrates the nine races of the Seaside Sparrow, and a recording prepared by J. W. Hardy supplements two papers on vocalizations.

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A Late Pleistocene Vertebrate Assemblage from the St. Marks River, Wakulla County, Florida

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ABSTRACT—The St. Marks River in the central panhandle of Florida contains a well known, apparently late Pleistocene vertebrate assemblage that has been only superficially examined and reported. Previous collections are reviewed, and we report on new fossil materials recently obtained. Included are 37 species of mammals, 26 birds, 13 reptiles, 2 amphibians, and 9 fish. Of these, 14 species of mammals and 2 reptiles are limited solely to the Pleistocene. The fauna is mixed and reflects heterochronous deposition over time beginning at least in the late Pleistocene (Wisconsinan) and extending through the Recent. The species present reflect mixed woodland and grassland terrestrial communities as well as mixed estuarine and freshwater aquatic communities. The St. Marks River assemblage compares well to other contemporaneous late Pleistocene Florida panhandle sites. One extralimital taxa is reported, *Pyloodictic* cf. *P. olivaris*, the flathead catfish, whose natural range has not been reported east of the Mobile Bay drainage basin.

Florida is characterized by a number of rich and well documented Pleistocene vertebrate assemblages (Webb 1974a, Lundelius et al. 1983, Webb and Wilkins 1984) that contain a mixture of extant and extinct South American immigrant and North American endemic species. The majority of these sites are distributed throughout the peninsular portion of the State (Webb 1974a, Webb and Wilkins 1984). However, with the exceptions of Wakulla Springs (Brodkorb 1963, Webb 1974a), Chipola River (Martin 1969, Webb 1974a), and Aucilla River (Olson 1972, Webb 1974a, Gillette 1976a) very little attention has been devoted to sites on the panhandle of Florida. The St. Marks River, located 32 km south of Tallahassee in Wakulla County, is a particularly rich, late Pleistocene panhandle site that has only been superficially investigated (Gillette 1976b, Steadman 1980).

Leidy (1870), who reported on the occurrence of *Mammuthus columbi* (now *M. jeffersonii*), provided the first record of vertebrate fossil remains recovered from the St. Marks River, though the exact locality was not given. Subsequently, the St. Marks River has attracted

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numerous amateur collectors but a limited number of professionals. Storrs Olson (National Museum of Natural History) collected from a broad, shallow water area in Wakulla County near the Leon County line several times between 1968 and 1970. Tall Timbers Research Station sponsored collecting parties in the same area during 1974. Published accounts of the fauna are those of Gillette (1976b), who reported the mammals, and Steadman (1980), who discussed two specimens of *Meleagris gallopavo*. Storrs Olson (personal communication) examined the avian assemblage from the previous collections; however, he did not publish his findings.

With the exception of *Mammuthus* sp. *Mammut americanum*, *Synaptomys australis*, and possibly *Equus*, the majority of species from Gillette's (1976b) report are extant. Gillette (1976b) suggested that the assemblage was important because it represented a restricted temporal interval of the latest Pleistocene through the Holocene. Olsen (personal communication) felt the avian assemblage was very similar to that of today. Steadman (1980) characterized the site as a late Pleistocene deposit. The St. Marks River has also been reported by Lundelius et al. (1983) as being a naturally accumulating, fluvial Rancholabrean deposit.

The purpose of our study is to review previous collections and to report on new fossil materials recently obtained from the St. Marks River. We provide information regarding the paleoenvironment of the depositional area and compare the St. Marks River fauna to other late Pleistocene faunas in the region.

GEOLOGICAL AND GEOGRAPHIC SETTING

Florida consists of five naturally occurring topographical divisions (Cooke 1939:14). The St. Marks River drainage basin is in the coastal lowlands division. Although the panhandle of Florida shows a topographical record of the relict shorelines, no ages have been securely assigned to these formations (Winker and Howard 1977a,b). The coast line of the panhandle during the late Pleistocene is reported to be similar to that of today (Winker and Howard 1977b).

The St. Marks River is considered part of the Gulf Hammock region; it is underlain by the Upper Oligocene Suwannee Limestone (Harper 1914:302). The early Miocene St. Marks Formation overlies the Suwannee Formation in almost all of Wakulla County (Puri and Vernon 1964). The St. Marks Formation was revised to include the calcareous downdip facies of the Tampa Formation (Puri 1953). These formations can be found in many areas as outcroppings in springs and rivers (Spencer and Rupert 1987). The surface is mostly loamy

sand, probably Pleistocene in origin. The soil surrounding the river's edge is classified as Tooles-Nuttall fine sand that is frequently flooded (Spencer and Rupert 1987). Topographically the region is nearly level, except for a few hilly areas (Harper 1914:302). The whole area east of the Apalachicola River in Wakulla County is called the Woodville Karst Plain (Hendry and Sproul 1966, Yon 1966), characterized by sand dunes overlying limestone (Hendry and Sproul 1966:154).

The St. Marks River is fed by the St. Marks Spring located just inside Leon County (Fig. 1). Limestone lines the perimeter of the spring. The vent is located about 26 m below the water surface and has an average base flow of 14.7 m³/sec (Rosenau et al. 1977). This measurement was taken approximately 800 m down stream

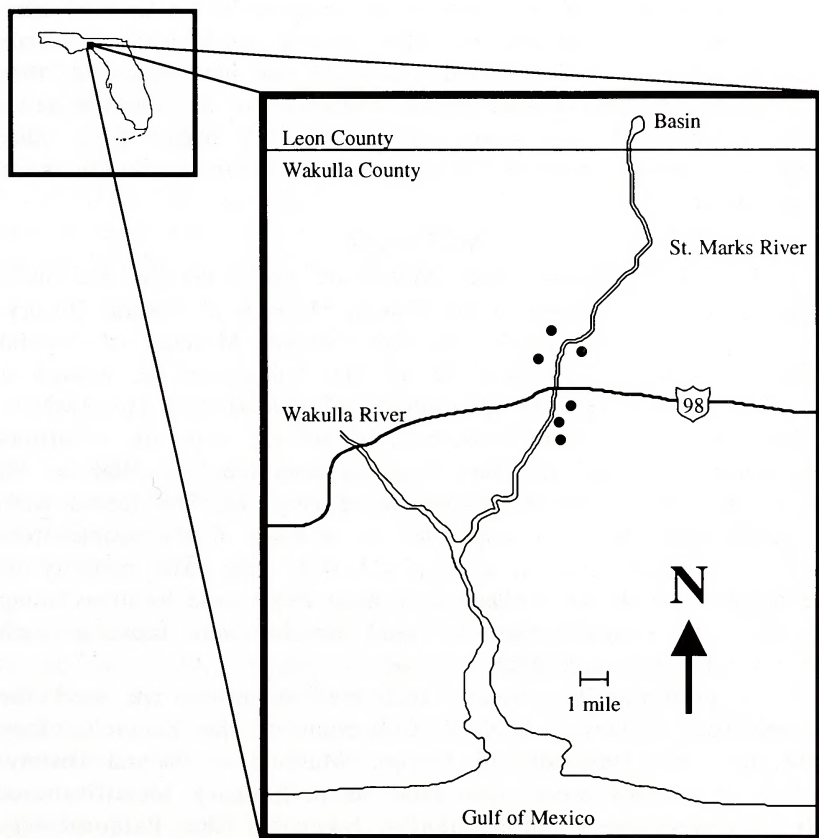


Fig. 1. St. Marks River in the central panhandle of Florida. Solid circles indicate 1987 collection sites.

from the main vent. The pH and temperature as measured 16 July 1974 were 7.6 and 21.0C, respectively. Newport Spring also feeds the river about 800 m north of the U.S. Highway 98 bridge. The discharge of the spring as measured 2 March 1972 was 0.23 m³/sec with a pH of 7.8 and water temperature of 19C (Rosenau et al. 1977).

Primary depositional site(s) were not located. The fossils are probably eroding out of the banks along much of the length of the river and washed down river by the current. Dense accumulations of fossils may be found in sand deposits, around submerged debris, and in deep holes along the entire length of the river.

The St. Marks River with its shallow, relatively clear waters with abundant fossil and archaeological materials has been a popular recreational S.C.U.B.A. diving area for the past 30 years. Local divers report huge quantities of fossils have been recovered by amateur collectors. One of us (J.L.) observed an entire pick-up truck load of fossils being removed in 1978. Local divers report that have collected "tons of it." Although several large private collections of St. Marks material exist, unfortunately they have been mixed with fossils from other regional aquatic systems which makes their inclusion here inappropriate.

METHODS

We made extensive new collections and reviewed previously collected materials housed at the Florida Museum of Natural History, University of Florida (UF), and the National Museum of Natural History (USNM), Washington, D. C. Our collections are housed at the University of Georgia Museum of Natural History (UGAMNH). Collection efforts were concentrated in six separate locations approximately 3.2 km in either direction from the U.S. Highway 98 bridge that crosses the St. Marks River (Fig. 1). The fossils were collected from 16 to 19 July 1987 by a team of six people from the University of Georgia using S.C.U.B.A. gear. The majority of the fossil materials was collected by hand from these locations along the river. In addition, extensive sand samples were taken at each site for subsequent screening.

To preliminarily identify recovered materials we used the Comparative Reference Skeletal Collection of the Zooarchaeology Laboratory, the University of Georgia Museum of Natural History. Reference sources were also used in preliminary identifications. All materials were subsequently taken to the Paleontology Laboratory, the Florida Museum of Natural History, University of Florida, to confirm identifications. Notes were made on the element identified, side, and fusion of bones where possible.

SYSTEMATIC PALEONTOLOGY

Standardized common and current scientific names follow Robins et al. (1991) for fishes; Collins (1990) for amphibians and reptiles; American Ornithologists' Union (1983) for birds, and Kurtén and Anderson (1980) and Jones et al. (1992) for mammals. Museum acronyms are indicated in the introduction. A complete faunal listing of the species recovered from the St. Marks site is provided in Table 1.

CLASS MAMMALIA

Order Didelphimorphia

Family Didelphidae

Didelphis virginiana Kerr

Virginia Opossum

Material—A single left dentary, UGAMNH1735.

Remarks—The single element is identical to that of modern *Didelphis virginiana*. This was the only marsupial species present in North America during the Pleistocene. It is known from numerous fossil sites in Florida (Webb 1974a). Its stratigraphic range includes Middle Blancan to Recent (Kurtén and Anderson 1980). It occurs in a variety of habitats, but it is usually found in forests and woodlands near water (Gardner 1973). We follow Marshall et al. (1990) in the use of the ordinal name Didelphimorphia as do Jones et al. (1992).

Order Xenarthra

Family Dasypodidae

Holmesina septentrionalis (Leidy)

Northern Pampathere

Material—Right astragulus, UGAMNH2012; right calcaneus, UGAMNH2159; right metacarpus II, UGAMNH1981; two phalanges, UGAMNH1982-1983; numerous dermal plates, UGAMNH1954-1980, 1984-2029, 2160, 2166.

Remarks—The species is known from numerous sites throughout the South and Southeast. Its range is somewhat similar to that of its modern relative, *Dasypus novemcinctus*, and *Holmsina* had a similar preference for open woodlands (Kurtén and Anderson 1980). Like its modern counterpart, *Holmsina* probably fed on insects and various invertebrates. Kurtén and Anderson (1980) suggest this diet might have restricted them to relatively warm climates where food was available year round. Specimen UHAMNH2159, a right calcaneus, has rodent and carnivore gnaw marks that occurred prior to fossilization. Its stratigraphic range is early Irvingtonian to Wisconsinan (Kurtén and Anderson 1980).

Table 1. List of vertebrate species recovered from the St. Marks River.
The figure † indicates extinct forms.

Class Mammalia

Order Didelphimorphia

- Family Didelphidae
Didelphis virginiana

Order Xenarthra

- Family Dasypodidae
†*Holmesina septentrionalis*
Family Megalonychidae
†*Megalonyx jeffersonii*
Family Mylodontidae
†*Glossotherium harlani*

Order Primates

- Family Hominidae
Homo sapiens

Order Lagomorpha

- Family Leporidae
Sylvilagus sp.

Order Rodentia

- Family Castoridae
Castor canadensis
Family Geomyidae
Geomys pinetis
Family Muridae
Microtus sp.
Microtus pinetorum
Neofiber alleni
Ondatra zibethicus
Synaptomys australis

Order Carnivora

- Family Mustelidae
Mustela sp.
Lutra canadensis
Mephitis mephitis
Family Canidae
Canis sp.
†*Canis dirus*
Urocyon cinereoargenteus
Family Procyonidae
Procyon lotor
Family Ursidae
Ursus cf. *U. americanus*
Family Felidae
Felis sp.
†*Smilodon* sp.

Order Proboscidea

- Family Mammutidae
†*Mammuthus jeffersonii*
Family Elephantidae
†*Mammut americanum*

Order Perissodactyla

- Family Equidae
Equus sp.
Family Tapiridae
†*Tapirus* sp.

Order Artiodactyla

- Family Tayassuidae
†*Platygonus compressus*
Family Suidae
Sus scrofa
Family Camelidae
†*Hemiauchenia macrocephala*
†*Palaeolama mirifica*
Family Cervidae
Odocoileus virginianus
Family Bovidae
Bison sp.
Bison bison
Bos taurus

Class Aves

Order Podicipediformes

- Family Podicipedidae
Podiceps auritus
Podilymbus podiceps

Order Pelecaniformes

- Family Phalacrocoracidae
Phalacrocorax auritus

Order Ciconiiformes

- Family Ardeidae
Ardea herodias
Butorides virescens
Egretta caerulea
Family Threskiornithidae
Eudocius albus

Order Anseriformes

- Family Anatidae
Aix sponsa
Anas acuta

Table 1. Continued.

<i>Anas americana</i>	Family Trionychidae
<i>Anas discors</i>	<i>Trionyx</i> sp.
<i>Anas platyrhynchos</i>	Order Squamata
<i>Anas</i> sp.	Family Colubridae
<i>Aythya collaris</i>	<i>Elaphe obsoleta</i>
<i>Aythya</i> sp.	Gen. et spec. indet.
<i>Branta canadensis</i>	Order Crocodilia
<i>Bucephala albeola</i>	Family Alligatoridae
<i>Lophodytes cucullatus</i>	<i>Alligator mississippiensis</i>
<i>Mergus merganser</i>	
Order Falconiformes	Class Amphibia
Family Accipitridae	Order Caudata
<i>Buteo jamaicensis</i>	Family Sirenidae
<i>Pandion haliaetus</i>	<i>Siren</i> sp.
Order Galliformes	Order Anura
Family Phasianidae	Gen. et spec. indet.
<i>Meleagris gallopavo</i>	
Order Gruiformes	Class Osteichthyii
Family Rallidae	Order Lepisosteiformes
<i>Fulica americana</i>	Family Lepisosteidae
<i>Gallinula chloropus</i>	<i>Lepisosteus</i> sp.
Family Aramididae	Order Amiiformes
<i>Aramus guarauna</i>	Family Amiidae
Order Strigiformes	<i>Amia calva</i>
Family Strigidae	Order Siluriformes
<i>Strix varia</i>	Family Ictaluridae
	<i>Pylodictis</i> cf. <i>P. olivaris</i>
Class Reptilia	Family Ariidae
Order Testudines	<i>Ariopsis felis</i>
Family Chelydridae	Order Salmoniformes
<i>Chelydra serpentina</i>	Esocidae
Family Kinosternidae	<i>Esox</i> sp.
Gen. et spec. indet.	Order Perciformes
Family Emydidae	Family Percichthyidae
<i>Pseudemys concinna</i>	<i>Morone saxatilis</i>
<i>Pseudemys floridanus</i>	Family Sparidae
<i>Pseudemys nelsoni</i>	<i>Archosargus probatocephalus</i>
<i>Trachemys scripta</i>	Family Sciaenidae
<i>Terrapene carolina</i>	<i>Sciaenops ocellatus</i>
<i>Terrapene carolina putnami</i>	Family Mugilidae
Family Testudinidae	<i>Mugil</i> sp.
<i>Geochelone incisa</i>	
<i>Geochelone</i> sp.	
<i>Gopherus polyphemus</i>	

Family Megalonychidae
Megalonyx jeffersonii (Desmarest)
Jefferson's Ground Sloth

Material—A single phalanx, UGAMNH2135, and tooth, UGAMNH2136.

Remarks—Jefferson's ground sloth occurred in woodlands where it apparently fed on nuts, berries, leaves, and twigs (Stock 1925). It is known from a number of sites in the Southeast including Florida (Webb 1974a), Georgia (Ray 1967), South Carolina (Hay 1923, Roth and Laerm 1980), and Tennessee (Guilday et al. 1969). It could have tolerated a seasonally cool climate as evidenced by its Pleistocene occurrence in what is now Canada and Alaska (McNab 1985). It is reported from Irvingtonian to Rancholabrean sites with a terminal date of 13,890 years B.P., although Kurtén and Anderson (1980) suggest it may have survived even longer in Florida.

Family Mylodontidae
Glossotherium harlani (Owen)
Harlan's Ground Sloth

Material—Two teeth, UGAMNH2137-2138.

Remarks—This was an open plains and grassland species (Stock 1925). It is reported from Irvingtonian to Rancholabrean sites with a terminal date of 13,890 years B.P., although Kurtén and Anderson (1980) suggest it may have survived even longer in Florida.

Order Primates
Family Hominidae
Homo sapiens Linnaeus
Human

Material—Cranial fragment, UF21280.

Remarks—This single specimen was recovered by Gillette (1976b). Unfortunately, the cranial fragment was not available for examination. We are, therefore, unable to comment on the degree of mineralization. No other human remains were recovered in our efforts. The presence of considerable amounts of Native American cultural material (pottery shards) as well as 18-20th century European-American artifacts indicates the St. Marks River was a site of human occupation before and after European contact.

Order Lagomorpha
Family Leporidae
Sylvilagus sp. indet.

Material—Tooth fragment, UF21301.

Remarks—Rabbits are a common component of most Pleistocene sites in Florida. It is surprising no more than a single tooth fragment was encountered in the St. Marks River material. Two species of rabbit occur in the St. Marks region today, the eastern cottontail, *Sylvilagus floridanus*, and the more common swamp rabbit, *S. aquaticus*. The former prefers heavy brushy, forested areas with open areas nearby and edges of swamps. The latter is most common in marshes, swamps, and bottomlands (Golley 1962).

Order Rodentia
Family Castoridae
Castor canadensis Kuhl
Beaver

Material—Left ulna, UGAMNH2126; right upper molar, UGAMNH2125; right M³, UGAMNH2124; four molars, UF21294.

Remarks—Two beaver species occurred in Florida in the late Pleistocene, *Castoroides ohioensis* and *Castor canadensis*. Both have even been found in the same deposits (Webb 1974a); however, only the latter is represented in the St. Marks River fauna. The beaver is found in any suitable water habitat including rivers, streams, lakes, and marshes (Lowery 1974). Its relative rarity in the St. Marks may be related to the presence of *Alligator*. The stratigraphic range is late Blancan to Recent (Kurtén and Anderson 1980).

Family Geomyidae
Geomys pinetis Rafinesque
Southeastern Pocket Gopher

Material—A single lower fourth premolar, UF21291.

Remarks—*Geomys pinetis* is the only species of pocket gopher in the Southeast. It is associated with the sandy soils of the Coastal Plain (Golley 1962) and is present today in the uplands adjacent the St. Marks River. It is known from late Irvingtonian to Recent (Kurtén and Anderson 1980).

Family Muridae
Microtus sp. indet.

Material—Left M³, UGAMNH2127.

Remarks—This fragment, while certainly *Microtus*, could not be

referred to a species with confidence. We follow Jones et al. (1992) in their use of the familial name Muridae.

Microtus pinetorum (LeConte)

Pine Vole

Material—Right M², UGAMNH2128.

Remarks—This molar compares well to modern *Microtus pinetorum*. Regionally, the pine vole can be found in a wide range of habitats from hardwood and pine forests to overgrown fields (Golley 1962). The stratigraphic range is Sangamonian to Recent (Kurtén and Anderson 1980).

Neofiber alleni True

Round-tailed Muskrat

Material—right M², UGAMNH2121; right M³, UGAMNH2123; right M₃, UGAMNH2122; maxilla, UF21293.

Remarks—*Neofiber alleni* is a semi-aquatic mammal that prefers permanent bodies of water with emergent aquatic vegetation (Frazier 1977). Although it has a restricted range today, essentially extreme northern Florida and south Georgia, during the Pleistocene it ranged as far west as Kansas (Hibbard 1943). It is reported from late Irvingtonian to Recent (Kurtén and Anderson 1980). The stratigraphic range is Illinoian to Recent (Kurtén and Anderson 1980).

Ondatra zibethicus (Linnaeus)

Muskrat

Material—Right dentary with M¹ AND M², UGAMNH2120; dentary, UF21292.

Remarks—The muskrat, like the round-tailed muskrat, is a semi-aquatic mammal that prefers permanent bodies of water (Nelson and Semken 1970). There is not overlap in the range of the two species today. However, Martin and Webb (1974) indicate they were sympatric in at least two late Pleistocene Florida faunas, Devils Den and Ichetucknee River. The occurrence of the two species in the St. Marks River fauna is not overly suggestive that they were sympatric here in the past because of the apparently heterochronous deposition at St. Marks. Furthermore, although the muskrat does not presently occur in the St. Marks River or Apalachicola River drainages, it is known from the extreme western panhandle and the Upper Coastal Plain of Georgia, a distance of 120 km.

Synaptomys australis Simpson

Florida Bog Lemming

Material—Left mandible with M₁, UF21295.

Remarks—The specimen referred to in Gillette's (1976b) review of the St. Marks River is the only record of this species at the site. In Florida it is known primarily from Sangamonian and Wisconsinan assemblages, although elsewhere it is known from the Illinoian through the Wisconsinan (Kurtén and Anderson 1980). Its presence at Devils Den suggests it might have persisted until about 8,000 years B.P. (Martin and Webb 1974), although this radiocarbon date is considered suspect. The Florida bog lemming is similar morphologically to *S. cooperi*, the northern bog lemming, but differs considerably in size; it is about 35% larger than *S. cooperi*. Kurtén and Anderson (1980) suggest it might represent a clinal variate of *S. cooperi*. It was an inhabitant of moist bogs and damp meadows (Burt 1928).

Order Carnivora

cf. Order Carnivora, gen. et sp. indet.

Material—A left coronoid, UGAMNH1881.

Remarks—This specimen, though carnivore-like, could not be identified to the familial level.

Family Mustelidae

Mustela sp. indet.

cf. Weasel

Material—A single left humerus, UGAMNH1738 and right P³, UGAMNH1736.

Remarks—Two species of weasel, *Mustela frenata* and *M. vison*, are common to the region today. Both are known from the Irvingtonian to Recent and are represented in regional fossil sites (Webb 1974a). However, fossil weasels have been reported from very few sites in Florida (Martin 1974, Webb 1974a).

Lutra canadensis (Shreber)

River Otter

Material—Left humerus, UGAMNH1741.

Remarks—This material compares well to modern *Lutra canadensis*. The stratigraphic range includes early Irvingtonian to Recent, and the species is represented in numerous regional sites (Kurtén and Anderson 1980). The species occurs in woodlands near rivers and streams but is also known from tidal creeks and marshlands (Lowery 1974).

Mephitis mephitis (Schreber)

Striped Skunk

Material—Right mandible, UGAMNH1746; left humerus, UGAMNH1737.

Remarks—This material compares well to modern *Mephitis mephitis*, which can be found in mixed woodlands, brushlands, or prairies but generally in reasonable proximity to water (Lowery 1974). The stratigraphic range is mid Blancan to Recent (Kurtén and Anderson 1980).

Family Canidae

Canis sp. indet.

Material—Left ilium, UGAMNH1739; right dentary, UGAMNH1878, 1880; right scapula, UGAMNH1879.

Remarks—None of these elements could be identified beyond the generic level. They are well mineralized, suggesting they are not modern *C. familiaris* contaminants. Several species of *Canis* are known from late Pleistocene sites in Florida. These include *C. lupus*, the gray wolf; *C. rufus*, the red wolf; *C. latrans*, the coyote; and *C. dirus*, the dire wolf. Martin (1974) has concluded that only two species, *C. rufus* and *C. dirus*, are common to middle and late Pleistocene deposits of Florida. *Canis lupus* is typical of Irvingtonian deposits, whereas *C. dirus* is representative of the Rancholabrean.

Canis dirus Leidy

Dire Wolf

Material—left radius, UGAMNH1877.

Remarks—*Canis dirus* is known from a number of late Pleistocene sites in Florida (Webb 1974a) and is one of the more common species of mammals at numerous Rancholabrean sites throughout North America. It is thought to have inhabited a wide range of habitats because it was a hunter and scavenger (Kurtén and Anderson 1980, Lundelius et al. 1983). The stratigraphic range is early Illinoian to Wisconsinan (Kurtén and Anderson 1980). The most recent terminal date for extinction is given at about 8,000 years B.P. in Florida (Martin and Webb 1974), but somewhat earlier (approximately 9,000-10,000 year B.P.) elsewhere (Kurtén and Anderson 1980).

Urocyon cinereoargenteus (Shreber)

Gray Fox

Material—Right dentary, UGAMNH1743; left frontal, UGAMNH1744.

Remarks—This material is not well mineralized, which suggests that it is a modern contaminant. However, *Urocyon cinereoargenteus* would be expected in this fauna. It can be found in a wide range of habitats today, but brushy and woody areas probably best describe the preferred habitat in the South and Gulf Coast area (Lowery 1974). The stratigraphic range in Florida is Middle Rancholabrean to Recent (Martin and Webb 1974). Elsewhere it is known as early as the Blancan (Kurtén and Anderson 1980).

Family Procyonidae
Procyon lotor (Linnaeus)
Raccoon

Material—Three left dentaries, UGAMNH1742, 1747, 1750. A partial skeleton is represented by UF21296.

Remarks—The University of Georgia material is not well mineralized, which suggests it could be a modern contaminant, since *Procyon lotor* is part of the modern fauna. In the Florida panhandle today, the racoon is an inhabitant of forested bottomland swamps. Its fossil record in Florida extends from the Late Irvingtonian to Recent (Martin and Webb 1974).

Family Ursidae
Ursidae gen. et sp. indet.

Material—Three phalanges, UGAMNH1745, 1749, 1752.

Remarks—Generic identity of this material is uncertain. In addition to the modern black bear, *Ursus americanus* Pallas, several extinct species of bears are known from the Pleistocene of Florida. These include the cave bear, *Tremarctos floridanus* (Gidley), and the lesser short-faced bear, *Arctodus pristinus* Leidy, all of which persisted at least until the late Wisconsin (Kurtén and Anderson 1980).

Ursus cf. *U. americanus* Pallas
cf. Black Bear

Material—A single right dentary with M₁, UGAMNH1751.

Remarks—This specimen is well mineralized, but it is too worn for positive identification. The black bear can be found in forests and bottomland swamps throughout much of the Southeast (Golley 1962, Lowery 1974). It is represented in numerous late Pleistocene sites. The stratigraphic range is early Irvingtonian to Recent (Kurtén and Anderson 1980).

Family Felidae

Felis sp. indet.

Material—Left radius, UGAMNH1740.

Remarks—This specimen is a large *Felis*, but it is too worn for positive identification. Webb (1974a) states that several species of *Felis* are known from the Late Pleistocene of Florida, and include *F. atrox* Leidy, *F. concolor* Linnaeus, *F. onca* (Linnaeus), *F. pardalis* Linnaeus, *F. rufus* Schreber, and *F. yagouaroundi* Geoffroy. Another possibility is *Felis amnicola*, a new, small cat described by Gillette (1976a). The description is based on several specimens from various localities in Florida and possibly Georgia.

Smilodon sp. indet.

Material—Left scapho-lunar, UGAMNH1748.

Remarks—The sabertooth cats are reported from a dozen or more late Pleistocene sites in Florida (Webb 1974a, Kurtén and Anderson 1980). Slaughter (1963) proposed a series of successional changes in *Smilodon* species throughout the North American Pleistocene. Webb (1974a) concurs that records of *Smilodon* in Florida support such a successional outline: *Smilodon gracilis* is a late Blancan and early Irvingtonian; *S. fatalis* is representative of late Irvingtonian and early Rancholabrean sites; and that *S. floridanus* is typical of the late Rancholabrean. The temporal span reflected by other faunal elements from the St. Marks would be more suggestive of the latter species; however, given the similarity of these species, more precise identification is impossible from the limited available material. *Smilodon* could probably have been found in habitats ranging from grassland to woodland (Merriam and Stock 1932, Lundelius et al. 1983).

Order Proboscidea

Proboscidea gen. et sp. indet.

Material—Sesamoid, UGAMNH1098; tusk fragment, UF21255; skull fragment, UF21256; leg fragment, UF21257; vertebral fragment UF21258.

Remarks—These specimens are very definitely proboscidian, but assignment to species is impossible.

Family Mammutidae

Mammut americanum (Kerr)

American Mastodon

Material—Axis fragment, UGAMNH1614; tooth fragments, UGAMNH1612, 1613, 1615, 1616, UF21267 and 21276; tusk fragments, UF21277-21278; proximal humerus, UF21279; calcaneus, UF21290.

Remarks—The morphology of the elements is consistent with its identification as *Mammuth americanum*. Dreimanis (1968) suggested that *M. americanum* inhabited coniferous forests. The stratigraphic range is early Blancan to Wisconsinan (Kurtén and Anderson 1980).

Family Elephantidae
Mammuthus jeffersonii (Osborn)
Jefferson's Mammoth

Material—Tooth fragments, UGAMNH1607-1611; tooth fragments, UF21259-21262, 21264-21266; mandibular symphysis, UF21263.

Remarks—The morphology of the tooth fragments and mandibular symphysis is consistent with its identification as *Mammuthus jeffersonii*. Jefferson's mammoth probably inhabited open grasslands (Stock 1963, Harrington et al. 1974). The stratigraphic range is Illinoian to Wisconsinan (Kurtén and Anderson 1980).

Order Perissodactyla
Family Equidae
Equus sp. indet.
Horse

Material—left astragalus, UGAMNH1035; cervical vertebra, UGAMNH1170; left upper cheek tooth, UGAMNH1045; right upper cheek tooth, UGAMNH1031; right lower cheek tooth, UGAMNH1048; cheek tooth, UGAMNH1046, 1047, 1062; right deciduous P², UGAMNH1042; left deciduous P², UGAMNH1061; right cuneiform, UGAMNH1049; left femoral head, UGAMNH1034; right distal humeral epiphysis, UGAMNH1054; left I₃, UGAMNH1036; right I², UGAMNH1041; lower incisor, UGAMNH1056; left I³, UGAMNH1059; left I¹, UGAMNH1060; incisive fragment, UGAMNH1032; left upper molar, UGAMNH1038; right M², UGAMNH1039; right M₃, UGAMNH1044; left M³, UGAMNH1057; upper molar fragment UGAMNH1029; left navicular, UGAMNH1063; medial phalanges UGAMNH1030, 1050, 1053; distal phalanx, UGAMNH1051; proximal phalanx, UGAMNH1055; left P², UGAMNH1037; right P², UGAMNH1040; left upper premolar, UGAMNH1043; right lower premolar, UGAMNH1058; left scapula, UGAMNH1052; sesamoid, UGAMNH1033; medial phalanx, UF21228; teeth, UF21229-21238; teeth UF21240-UF21254; cheek tooth, axis, and pelvis, UF21297.

Remarks—*Equus* is well represented in St. Marks River. A portion of the material is poorly mineralized and probably represent contaminants of the modern *E. caballus*. However, the majority of elements are well fossilized, and it is likely that most of the material

is of late Pleistocene origin. Given the uncertain relationships of late Pleistocene horses in general and the likelihood of heterochronous deposition, we did not assign the material to a particular species. Pleistocene *Equus* was generally a grassland species (Kurtén and Anderson 1980).

Family Tapiridae

Tapiridae gen. et spec. indet.

Material—Left dentary, UGAMNH2068.

Remarks—This edentulous specimen could not be assigned to *Tapirus* with confidence, although the morphology is similar.

Tapirus sp. indet.

Tapir

Material—Right upper deciduous premolar, UGAMNH2070, left upper deciduous premolar, UGAMNH2071; right fibula, UGAMNH2069.

Remarks—The available material, while certainly *Tapirus*, could not be referred to a species with confidence. Tapirs occur in wet woodlands (Simpson 1945, Gray and Crammer 1961).

Order Artiodactyla

Family Tayassuidae

Platygonus compressus LeConte

Flat-headed Peccary

Material—Axis, UGAMNH2072.

Remarks—The material has the diagnostic characters of *Platygonus compressus* which is thought to have wide environmental tolerances, but was probably most associated with open woodlands (Martin and Guilday 1967, Ray et al. 1970). The stratigraphic range is Sangamonian to Wisconsinan (Kurtén and Anderson 1980).

Family Suidae

Sus scrofa Linnaeus

Pig

Material—Left maxilla with P³ and P⁴, UGAMNH1159; right humeral fragment, UGAMNH1160; right femoral diaphysis, UGAMNH1162; right radial fragment, UGAMNH1161; left humeral fragments, UGAMNH1163, 1158; right ilial fragment, UGAMNH1157; distal humeral fragment, UGAMNH1178; left femur, UGAMNH1156.

Remarks—None of the pig material showed evidence of significant mineralization. The pig was introduced during historic times and represents a domesticate. Specimen UGAMNH1178 shows marks of a saw.

Family Camelidae

Camelidae gen. et sp. indet.

Material—Proximal phalanges, UGAMNH1647, 1648; right scaphoid, UGAMNH1649; right astragalus, UGAMNH1650; right scapula, UGAMNH1651; left proximal femoral fragment, UGAMNH1652.

Remarks—These specimens have distinctive camelid familial characters, but cannot be assigned to a particular species.

Hemiauchenia macrocephala (Cope)

Large-headed Llama

Material—Proximal phalanges, UGAMNH2151, 2152.

Remarks—The identification of these elements to *Hemiauchenia macrocephala* is based on the size of the phalanges. According to Webb (1974b), *H. macrocephala* was a plains and grasslands inhabitant. The stratigraphic range is Wisconsinan to Recent (Kurtén and Anderson 1980). Because this species has such a limited stratigraphic range, at least a portion of the deposit can be correlated to the Wisconsinan.

Paleolama mirifica (Simpson)

Stout-legged Llama

Material—Left proximal metacarpal fragment, UGAMNH2146; right humerus, UGAMNH2145; left metatarsus, UGAMNH2158; left M₃, UGAMNH2147; metapodial, UGAMNH2148; right distal humerus, UGAMNH2149; left pisiform, UGAMNH2150.

Remarks—The stratigraphic range is late Irvingtonian to Wisconsinan (Kurtén and Anderson 1980). Webb (1974b) reports them to be an inhabitant of grasslands and savannahs. Specimen UGAMNH2158, a left metatarsus, has longitudinal cracks indicative of weathering prior to fossilization.

Family Cervidae

Odocoileus virginianus (Zimmerman)

White-tailed Deer

Material—Antler fragments, UGAMNH1103, 1106, 1134, 1148; left astragalus, UGAMNH1101, 1124, 1210, 1757; right astragalus, UGAMNH1071, 1113, 1125, 1677, 1758, 2162; right calcaneus, UGAMNH1150, 1181, 1204, 1756; left calcaneus, UGAMNH1069, 1073, 1077, 1079, 1205, 1653, 2153, 2154, 1667, 1678; right cubonavicular, UGAMNH1074, 1111; right dentary with P₁, P₂, P₃, M₂, M₃, UGAMNH1081; left dentary with M₁, UGAMNH1131; right dentary with M₁, M₂, M₃, UGAMNH1108, 1126; right dentary with P₂, P₃, M₁, M₂, M₃, UGAMNH1191; right proximal femoral fragment, UGAMNH1184; femoral diaphysis, UGAMNH1064; left femoral head,

UGAMNH1129; left femoral diaphysis, UGAMNH2163; right distal femur, UGAMNH11139; left distal femoral fragment, UGAMNH1085, 1088; left femoral lesser trochanter, UGAMNH1130; right femoral diaphysis, UGAMNH1139, 2164; right frontal with antler, UGAMNH1068, 1099; left frontal with antler, UGAMNH1012, 1082, 1118, 1121, 1666; frontal with antler pedicle, UGAMNH1196, 1203; right humeral fragments, UGAMNH1075, 1100, 1122, 1133, 1142, 1661, 1668; left humeral fragments, UGAMNH1070, 1093, 1136, 1137, 1143, 1185, 1186, 1235, 1679; right ilial fragments, UGAMNH1076, 1090, 1681; left ilial fragments, UGAMNH1079, 1086, 1147; left ischial fragments, UGAMNH1105, 1119, 1682; right lunate, UGAMNH1112; right maxilla with P⁴, M¹, UGAMNH1206; left metacarpal fragments, UGAMNH1087, 1102, 1114, 1115, 1146, 1180, 1198, 1663; right metacarpal fragments, UGAMNH1072, 1084, 1092, 1097, 1116, 1665; metacarpal diaphysial fragments, UGAMNH1104, 1193-1195, 1670; right metatarsal fragments, UGAMNH1091, 1183, 1201, 1659, 1669, 1675, 1759; metatarsal diaphysial fragments, UGAMNH1117, 1199, 1200, 1208, 1212, 1656, 1672, 1673, 1676;

left metatarsal fragments, UGAMNH1120, 1192, 1654, 1655, 1662, 1664, 1671; right M¹, UGAMNH1109, UGAMNH1151; left M³, UGAMNH1289; right M³, UGAMNH1190; left petrous, UGAMNH1110, 1128, 1202, 1214; medial phalanx, UGAMNH1080, 1141, 1209, 1213, 1753, 1754; proximal phalanx, UGAMNH1078, 1109, 1127, 1182, UGAMNH1211, 1755; left radial fragment, UGAMNH1065; right radial diaphysial fragment, UGAMNH1067; left radial fragments, UGAMNH1207, 2165; right radial fragments, UGAMNH1144; sacrum, UGAMNH1089; left scapular fragments, UGAMNH1140, 1188; right scapular fragments, UGAMNH1094, 1145; right distal tibial fragments, UGAMNH1095, 1123, 1658, 1680; left distal tibial fragments, UGAMNH1096, 1657; left proximal tibial fragment, UGAMNH1674; right proximal ulnar fragment, UGAMNH1132; left proximal ulnar fragment, UGAMNH1197; thoracic vertebral fragment, UGAMNH1760; lumbar vertebral fragment, UGAMNH1187; cervical vertebral fragment, UGAMNH1066; atlas fragments, UGAMNH1083, 1149; axial fragment, UGAMNH1660; antler, UF21289; five mandibles, UF21298.

Remarks—The deer material shows a considerable range of mineralization. A significant portion is poorly mineralized and probably represents modern contaminants. The remaining material, however, is well mineralized, but mineralization alone is a poor indicator of possible Pleistocene age. The stratigraphic range of species is middle Blancan to Recent (Kurtén and Anderson 1980). *Odocoileus* is a woodland and forest edge species (Golley 1962, Lowery 1974, Lundelius et al. 1983).

Family Bovidae
Bovidae gen. et sp. indet.

Material—Proximal phalanges, UGAMNH1621, 1627, 1631, 1632; left lunate, UGAMNH1633, 1634; left lunar, UGAMNH1625; left scapular spine, UGAMNH1635; rib head, UGAMNH1636; right scapula, UGAMNH1622; right P₄, UGAMNH1623; left distal humerus, UGAMNH1624; left proximal femur, UGAMNH1626; right distal humeral epiphysis, UGAMNH1628; metatarsal diaphysial fragment, UGAMNH1629; left proximal tibial fragment, UGAMNH1630; tooth fragments, UF21239, 21281, 21282, 21285, 21288; distal humerus, UF21283; horn core tip, UF21284.

Remarks—These elements are definitely bovid but the available material does not permit specific distinction.

Bison bison (Linnaeus)
Bison

Material—Right M₂, UGAMNH1620; left P₃, UGAMNH1619; left P₂, UGAMNH1618; right M₂, UGAMNH1617; molar UF2299.

Remarks—While Jones et al. (1992) have employed *Bos bison* for the American bison, we continue the traditional use of *Bison bison*. Two species of bison are known from Florida. The giant bison, *B. latifrons*, is known from Illinoian and Sangamonian and survived up until the late Wisconsinan. The American buffalo or bison, *B. bison*, was widespread throughout the Wisconsinan through the Recent (Kurtén and Anderson 1980). *Bison* is typically associated with grasslands, though in the Southeast may well have ranged into woodlands (Golley 1962, Stock 1963). It became extinct in the southeastern United States early in the 19th Century.

Bos taurus Linnaeus
Cow

Material—Right proximal humeral diaphysis, UGAMNH10863; left scapula, UGAMNH1155; left ilium, UGAMNH1152, 1154; right metatarsal diaphysis, UGAMNH1117; right proximal humerus, UGAMNH1177; right distal humerus, UGAMNH1176; orbital portion of right maxilla, UGAMNH1153; right proximal tibia, UGAMNH1171; right distal femoral epiphysis, UGAMNH1172; right astragalus, UGAMNH1173; distal phalanx, UGAMNH1174; metapodial, UF21300.

Remarks—*Bos taurus* was introduced into North America sometime after 1492. All elements were poorly mineralized. The presence of cow indicates the site has modern contaminants.

CLASS AVES

Order Podicipediformes

Family Podicipedidae

Podiceps auritus (Linnaeus)

Horned Grebe

Material—Distal portion of left ulna, USNM209968.

Remarks—Today the species winters in coastal areas and infrequently occurs in freshwater (Sprunt 1954).

Podilymbus podiceps (Linnaeus)

Pied-billed Grebe

Material—Right humerus, USNM210293, 210294, 210301, 210302; humerus, USNM210311; right proximal humerus, USNM210304; left humerus, USNM210307; left tibial fragments, USNM210292, 210308, 210309, 210315, 210322, 210325, 210327; right tibia, USNM210297, 210300, 210312, 210316, 210317; left ulna, USNM210296, 210303, 210305, 210306, 210310, 210328, 210329; right ulna USNM210313, 210321; radius, USNM210298; right coracoid, USNM210319; left coracoid, USNM210320; left femur, USNM210298; right carpometacarpus, USNM210321; left carpometacarpus, USNM210323; scapula, USNM210324; pedal phalanx, USNM210326; tarsometatarsus, USNM210314, 210318; left tibia, USNM210306.

Remarks—The species inhabits freshwater marshes and ponds, but also is associated with saltwater in winter (Sprunt 1954).

Order Pelecaniformes

Family Phalacrocoracidae

Phalacrocorax auritus (Lesson)

Double-crested Cormorant

Material—Left radius, USNM209845; left ulna, USNM209844; scapula, USNM209859; anterior sternum, USNM209843; left coracoid, USNM209858; phalanx 1 of digit II, USNM209861, 209852; phalanx 2 of digit II, USNM209856; left humerus, USNM209846; right humerus, USNM209851; proximal radius, USNM209860; right ulna, USNM209852; distal tibia, USNM209848; right femur, USNM209854; right mandible, USNM209855; left mandible, USNM209850; sternal fragment, USNM209857; left coracoid, USNM209849; right coracoid, USNM209847.

Remarks—This species is distributed in large rivers and lakes as well as brackish and saltwater systems (Sprunt 1954).

Order Ciconiformes
Family Ardeidae
Ardea herodias Linnaeus
Great Blue Heron

Material—Cervical vertebrae, USNM210282, 210283, 210285, 210287; right mandible, USNM210281; mandible fragments, USNM210280, 210286, 210288; maxilla fragment, USNM210279; right coracoid, USNM210291; right proximal humerus, USNM210289; distal tarsometatarsus, USNM210290; right carpometacarpus, USNM210279.

Remarks—The great blue heron has wide ecological tolerances, occurring in freshwater swamps and riparian habitats as well as saltwater marshes (Sprunt 1954).

Butorides striatus (Linnaeus)
Green-backed Heron

Material—Right humerus, USNM209966.

Remarks—*Butorides striatus* and *B. virescens*, sometimes regarded as separate species, are recognized as geographic races of *B. striatus* by the American Ornithologists Union (1983). It occurs along lake margins, streams, ponds, and freshwater and saltwater marshes (Sprunt 1954).

Egretta caerulea (Linnaeus)
Little Blue Heron

Material—Mandibular tip with right ramus, USNM209862.

Remarks—Freshwater swamps and saltwater marshes are the preferred habitats (Sprunt 1954).

Family Threskiornithidae
Eudocimus albus (Linnaeus)
White Ibis

Material—Right humerus, USNM209971; left proximal coracoid, USNM209972.

Remarks—*Eudocibus albus* is associated with swampy forests, marshy sloughs, and saltwater marshes (Sprunt 1954).

Order Anseriformes
Family Anatidae
Aix sponsa (Linnaeus)
Wood Duck

Material—Right carpometacarpus, USNM209931, 209938, 209939, 209944; left carpometacarpus, USNM209934; right ulna,

USNM209927, 209946; left ulna, USNM209926, 209940, 209945; left humerus, USNM209928, 209930, 209932, 209933; right humerus, USNM209941; radius, USNM209929, 209936; scapula, USNM209942, 209943; proximal tibia, USNM209935; right coracoid, USNM20992; right femur, USNM209925; right tarsometatarsus, USNM209937.

Remarks—The species is common today in freshwater woodland rivers, ponds, and marshes (Sprunt 1954).

Anas sp. indet.

Material—Right ulna, UGAMNH2078.

Anas acuta Linnaeus

North Pintail

Material—Left coracoid, USNM209965.

Remarks—The pintail is associated with freshwater marshes, ponds, and lakes (Sprunt 1954).

Anas americana Gmelin

American Wigeon

Material—Left humerus, USNM210270; left ulna, USNM210267, 210273; right scapula, USNM210278; scapula USNM210272, 210274; right coracoid, USNM210268, 210275, 210276; right ulna, USNM210277; phalanx 1 of digit II, USNM210269; radius, USNM210271.

Remarks—This species is an inhabitant of freshwater marshes, ponds, and shallow lakes (Sprunt 1954).

Anas discors Linnaeus

Blue-winged Teal

Material—Left carpometacarpus, USNM209865, 209866, 209872-209874; right carpometacarpus, USNM209870, 209871; right humerus, USNM209869; right coracoid, USNM209868; left ulna, USNM209864.

Remarks—Sprunt (1954) reports the species from freshwater ponds and lakes.

Anas platyrhynchos Linnaeus

Mallard

Material—Left humerus, USNM209910, 209911, 209914; right humerus, USNM209913, 209918; right scapula, USNM209916; left scapula, USNM209917; left coracoid, USNM209919; right coracoid, USNM209912; right carpometacarpus, USNM209920; furcula, USNM209915.

Remarks—The mallard prefers freshwater lakes and marshes (Sprunt 1954).

Aythya sp. indet.

Material—Right carpometacarpus, UGAMNH2073; left distal tibiotarsus, UGAMNH2077.

Aythya collaris (Donovan)

Ring-necked Duck

Material—Humerus shaft, USNM209899; left humerus, USNM209884, 209878, 209886, 209890, 209894, USNM209910; right humerus, USNM209877, 209893, 209903; left ulna, 209885, 209888, 209897; right ulna, USNM209878, 209892, 209905-209907; left tibia, USNM209880, 209908; right tibia, USNM209909; left carpometacarpus, 209898, 209900; right tarsometatarsus, USNM209881, 209889; left tarsometatarsus, USNM209887; tarsometatarsus, USNM209902; right coracoid, 209895, 209896; proximal radius, USNM209882; distal radius, USNM209883; radius, USNM209904; right scapula, USNM209891; cervical vertebra, USNM209901.

Remarks—This species is associated most commonly with wooded lakes, ponds, and rivers, but also is reported from saltwater systems (Sprunt 1954).

Branta canadensis (Linnaeus)

Canada Goose

Material—Right coracoid, UGAMNH2074; right tarsometatarsus, USNM209875; right distal carpometacarpus, USNM209876.

Remarks—Both USNM specimens from the 1970s are noted by Storrs Olson (personal communication) as small and possibly represent either a small subspecies or juveniles. The UGAMNH specimen from 1987 is large. Sprunt (1954:53) states the center of abundance in Florida for modern *Branta canadensis* is the St. Marks Refuge. This coracoid could possibly be assigned to *Branta* cf. *B. dickeyi* on the basis of size. Steven Emslie (Point Reyes Bird Observatory, personal communication) examined the St. Marks River specimen and thought it could be assigned to *B. dickeyi*. Measurements of the coracoid are larger than modern *B. canadensis*, but there is some overlap. Emslie (personal communication) reported a large *B. dickeyi* from the early Pleistocene of Florida. We refer the coracoid conservatively to *B. canadensis*. The species prefers freshwater lakes, rivers, and marshes (Sprunt 1954).

Bucephala albeola (Linnaeus)

Bufflehead

Material—Right carpometacarpus, USNM209969.

Remarks—The bufflehead is most common in saltwater bays and estuaries, and rarely in freshwater lakes and ponds (Sprunt 1954).

Lophodytes cucullatus (Linnaeus)

Hooded Merganser

Material—Right proximal humerus USNM209975; right distal humerus USNM209976, 209980; right humerus, USNM209977; left humerus, USNM209978; left ulna, USNM209979.

Remarks—The species occurs in freshwater wooded ponds, rivers, and lakes (Sprunt 1954).

Mergus merganser Linnaeus

Common Merganser

Material—Left distal tarsometatarsus, USNM209863.

Remarks—The common merganser inhabits wooded freshwater rivers and ponds but winters in saltwater bays (Sprunt 1954).

Order Falconiformes

Family Accipitridae

Pandion haliaetus (Linnaeus)

Osprey

Material—Right distal tarsometatarsus, USNM209967.

Remarks—The species prefers fresh and saltwater marshes, lakes, and bays (Sprunt 1954).

Buteo jamaicensis (Gmelin)

Red-tailed Hawk

Material—Left distal humerus, USNM209970.

Remarks—The red-tailed hawk is most common in deciduous forests adjacent to open grasslands (Sprunt 1954).

Order Galliformes

Family Phasianidae

Meleagris gallopavo Linnaeus

Wild Turkey

Material—Left tarsometatarsus, UGAMNH2075; right proximal tibiotarsus, USNM209921; right proximal femur, USNM209922; tarsometatarsus shaft, USNM209923.

Remarks—The species is known from drier swamps, open pine, and hardwoods as well as prairies (Sprunt 1954).

Order Gruiformes

Family Rallidae

Fulica americana (Gmelin)

American Coot

Material—Left distal tarsometatarsus, UGAMNH2076; left tibia, USNM209947, 209951; left distal tibiotarsus, USNM209956, 209958; right distal tibiotarsus, USNM20949, 209952, 209962; right tibiotarsus, USNM209961; tibiotarsus shaft, USNM209955; left ulna, USNM209954, 209966; right carpometacarpus, USNM209950, 209963; right distal femur, USNM209948; distal humerus, USNM209953; right scapula, USNM209959; left coracoid, USNM209960.

Remarks—The American coot is primarily associated with open freshwater ponds and marshes (Sprunt 1954).

Gallinula chloropus (Linnaeus)

Common Moorhen

Material—Right tarsometatarsus, USNM210259, 210260, 210255; right tibiotarsus, USNM210257; radius, USNM210256; left phalanx 1 of digit II, USNM210258.

Remarks—This species prefers freshwater marshes and ponds with heavy aquatic vegetation (Sprunt 1954).

Family Aramidae

Aramas guarauna (Linnaeus)

Limpkin

Material—Left tarsometatarsus, USNM210262, 210266; right tarsometatarsus, USNM210261; right distal tarsometatarsus, USNM210265; left distal tibiotarsus, USNM210263; right distal tibiotarsus, USNM210264.

Remarks—The limpkin is associated with open, freshwater swamps and marshes (Sprunt 1954).

Order Strigiformes

Family Strigidae

Strix varia Barton

Barred Owl

Material—Right proximal femur, USNM209973; right tibiotarsus shaft, USNM209974.

Remarks—The barred owl occurs in low, wet woodlands and swampy forests (Sprunt 1954).

CLASS REPTILIA

Order Testudines

Family Kinosternidae

Kinosternidae gen. et sp. indet.

Material—Nuchal, UGAMNH2038, 2047; right peripheral 1, UGAMNH2041; left peripheral 2, UGAMNH2042; left peripheral 4, UGAMNH2052; right peripheral 4, UGAMNH2044; left peripheral 9, UGAMNH2053; right peripheral 10, UGAMNH2048; plastron fragment, UGAMNH2050, 2051; right pleural 1, UGAMNH2039; left pleural 1, UGAMNH2045; right pleural 2, UGAMNH2043; right pleural 6, UGAMNH2040; pleural fragments, UGAMNH2046, 2049.

Remarks—None of the kinosternid material could be referred to genus or species.

Family Chelydridae

Chelydra serpentina (Linnaeus)

Snapping Turtle

Material—Right peripheral, UGAMNH2034, 2037; left peripheral 4, UGAMNH2035; peripheral UGAMNH2036.

Remarks—This material compares well with modern *Chelydra serpentina*. The species prefers permanent freshwater systems (Conant 1975).

Family Emydidae

Emydidae gen. et spec. indet.

Material—Right epiplastron, UGAMNH1350, 1351, 1355, 1356, 1366, 1368, 1370, 1402, 1403, 1405, 1444, 1462, 1482, 1510, 1530, 1535, 1538, 1546, 1548-1550, 1554, 1872; left epiplastron, UGAMNH1235, 1268, 1282, 1285, 1307, 1343, 1345, 1346, 1349, 1359, 1362, 1375, 1380, 1390, 1394, 1445, 1511, 1551; left humerus, UGAMNH1498; right hypoplastron at inguinal notch, UGAMNH1217, 1237, 1241, 1242, 1281, 1308, 1316, 1322, 1324, 1325, 1357, 1379, 1382, 1418, 1419, 1467, 1469, 1501, 1601, 1871; right hypoplastron at axillary notch, UGAMNH1238, 1240, 1301, 1352, 1358, 1404, 1452, 1474, 1503, 1547, 1553, 1555, 1565; right hypoplastron, UGAMNH1164, 1167, 1215, 1216, 1219, 1221, 1236, 1283, 1333, 1344, 1354, 1376, 1388, 1389, 1429, 1433, 1470, 1473, 1480, 1495, 1521, 1533, 1572, 1575, 1584, 1600, 1867, 1870; left hypoplastron at axial notch, UGAMNH1290, 1361, 1369, 1566, 1602; left hypoplastron at inguinal notch, UGAMNH1168, 1220, 1269, 1280, 1284, 1300, 1302, 1413, 1447, 1449, 1516, 1522, 1527, 1559, 1567, 1582; left hypoplastron, UGAMNH1218, 1222-1225, 1239, 1278, 1279, 1293, 1320, 1342, 1377, 1396, 1423, 1456, 1464, 1471,

1475, 1509, 1513, 1519, 1526, 1532, 1560, 1564, 1569, 1571, 1574, 1578, 1583; neural 1, UGAMNH1328, 1439, 1545, 1558; neural 2, UGAMNH1568, UGAMNH1588; neural 3, UGAMNH1573, 1581; neural 6, UGAMNH1461, 1577; neural 7, UGAMNH1260, 1341, 1579, 1874; neural 8, UGAMNH1271; neural 9, UGAMNH1410; neural, UGAMNH1233, 1258, 1259, 1277, 1291, 1309, 1310, 1312, 1363, 1364, 1372, 1384, 1392, 1393, 1406, 1409, 1414, 1440, 1441, 1494, 1524, 1563, 1570, 1576, 1580, 1589, 2139, 2141; nuchal, UGAMNH1261-1264, 1313, 1411, 1417, 1427, 1457, 1486, 1504, 1508, 1518, 1595; right peripheral 1, UGAMNH1165, 1321, 1399, 1398, 1451, 1489, 1525, 1528, 1592, 1866; left peripheral 1, UGAMNH1231, 1245, 1303, 1319, 1454, 1505, 1562; right peripheral 2, UGAMNH1381, 1397, 1407; left peripheral 2, UGAMNH1275, 1298, 1400; right peripheral 3, UGAMNH1169, 1294, 1442, 1531; left peripheral 3, UGAMNH1416, 1421, 1472; right peripheral 4, UGAMNH1540; left peripheral 4, UGAMNH2167; right peripheral 5, UGAMNH1395; left peripheral 5, UGAMNH1425, 1591; right peripheral 6, UGAMNH1244, 1517; left peripheral 6, UGAMNH1274, 1296, 1446;

right peripheral 7, UGAMNH1246, 1428, 1594; left peripheral 7, UGAMNH1329, 1432, 1453, 1455; right peripheral 8, UGAMNH1232, 1552, 2143; left peripheral 8, 1424, 1542; right peripheral 9, UGAMNH1166, 1373, 1484, 1490; left peripheral 9, UGAMNH1249, 1299, 1492; right peripheral 10, H1273, 1276; left peripheral 10, UGAMNH1248; right peripheral 11, UGAMNH1326, 1332, 1429, 1587, 1597; left peripheral 11, UGAMNH1297, 1304, 1408, 1435; peripheral UGAMNH1000, 1243, 1247, 1311, 1420, 1426, 1434, 1442, 1449, 1450, 1536, 1593, 1604; right pleural 1, UGAMNH1234, 1334, 1336, 1374, 1385, 1437, 1485, 1493, 1502, 1554, 1875; left pleural 1, UGAMNH1365, 1371, 1378, 1391, 1438, 1468, 1487, 1507, 2142; left pleural 2, UGAMNH1292; right pleural 2, UGAMNH1465, UGAMNH1491; left pleural 3, UGAMNH1431; right pleural 3, UGAMNH1436, UGAMNH1430; left pleural 4, UGAMNH1460; right pleural 5, UGAMNH1596; left pleural 5, UGAMNH1492; right pleural 6, UGAMNH1488; right pleural 7, UGAMNH1340; Pleural, UGAMNH1265-1267, 1270, 1286-1289, 1295, 1305, 1306, 1314, 1318, 1330, 1339, 1348, 1352, 1367, 1383, 1387, 1401, 1483, 1537, 1543, 1585, 1586, 1590, 1598, 1599, 1603, 1868, 1873; pygal, UGAMNH1317, 1323, 1422, 1458, 1476, 1556, 1561; left scapula, UGAMNH1496, 1497; right scapula, UGAMNH1665; suprapygal, UGAMNH1499; right xiphiplastron, UGAMNH1226-1230, 1250, 1251, 1253, 1255, 1257, 1331, 1347, 1360, 1415, 1463, 1472, 1479, 1481, 1869, 1876; left xiphiplastron, UGAMNH1252, 1254, 1256, 1315, 1335, 1337, 1338, 1386, 1512, 1514, 1515, 1523, 1539, 1544, 1459, 1478.

Remarks—Most of the emydid material could only be identified to the familial level. Species level identification is difficult and requires nearly complete elements. Almost all the material was well mineralized. We are confident that the majority represents Pleistocene deposition as opposed to Recent.

Pseudemys concinna (LeConte)

River Cooter

Material—Left peripheral 3, UGAMNH1882; left peripheral 4, UGAMNH1885; right peripheral 7, UGAMNH1884; right peripheral 11, UGAMNH1883.

Remarks—*Pseudemys concinna* is distinguished by its distinctive carapace. It is most common in slow streams and rivers (Conant 1975).

Pseudemys floridana (LeConte)

Cooter

Material—Left peripheral 3, UGAMNH2030; left pleural 3, UGAMNH2031; left pleural 4, UGAMNH2033; nuchal, UGAMNH2032.

Remarks—The species is most commonly associated with permanent bodies of freshwater including swamps and rivers (Conant 1975).

Pseudemys nelsoni Carr

Florida Redbelly Turtle

Material—Entoplastron, UGAMNH1904; right epiplastron, UGAMNH1920; right hypoplastron axial notch, UGAMNH1889, 1913, 1938; left hypoplastron axial notch UGAMNH1928, 1940; right hypoplastron inguinal notch, UGAMNH1908, 1943; left hypoplastron inguinal notch, UGAMNH1897, 1905; neural 7, UGAMNH1901; neural, UGAMNH1887; nuchal, UGAMNH1914, 1953; right peripheral 1, UGAMNH1899, 1906; right peripheral 2, UGAMNH1929; right peripheral 3, UGAMNH1937; left peripheral 3, UGAMNH1917; right peripheral 4, UGAMNH1930; left peripheral 5, UGAMNH1900; left peripheral 7, UGAMNH1890, 1898; right peripheral 8, UGAMNH1942, 1950; left peripheral 8, UGAMNH1945, 1948; right peripheral 9, UGAMNH1915; left peripheral 9, UGAMNH1886; left peripheral 10, UGAMNH1946, 1947; right peripheral 11, UGAMNH1506, 1918, 1919, 1941; left peripheral 11, UGAMNH1944; peripheral, UGAMNH1907, 1909, 1949; right pleural 1, UGAMNH1534, 1892, 1910; left pleural 1, UGAMNH1922, 1951, 2140; left pleural 2, UGAMNH1917; left pleural 3, UGAMNH1912; left pleural 4, UGAMNH1933; right pleural 5, UGAMNH1934; pleural, UGAMNH1891, 1893-1895, 1903, 1916,

1921, 1923-1927, 1931, UGAMNH1932, 1935, 1936, 1939; suprapygal, UGAMNH1888; right xiphiplastron, UGAMNH1896; left xiphiplastron UGAMNH1902, 1952.

Remarks—This is a species associated with freshwater sloughs, marshes, streams, and ponds (Conant 1975).

Trachemys scripta (Schoepff)

Slider

Material—Entoplastron, UGAMNH1763, 1792, 1801, 1831; right hypoplastron axial notch, UGAMNH1780; left hypoplastron axial notch, UGAMNH1828, 1833; right hypoplastron inguinal notch, UGAMNH1774; left hypoplastron inguinal notch, UGAMNH1819; neural 1, UGAMNH1790, 1834; neural 3, UGAMNH1789; neural 8, UGAMNH1846; neural, UGAMNH1766, 1769, 1819, 1837, 1842; nuchal, UGAMNH1520, 1764, 1773, 1776, 1778, 1782, 1784, 1787, 1791, 1823, 1841, 1844; right peripheral 1, UGAMNH1768, 1770, 1826, 1827; left peripheral 1, UGAMNH1783, 1840; right peripheral 2, UGAMNH1765, 1798, 1802; left peripheral 2, UGAMNH1776, 1806; right peripheral 3, UGAMNH1794; left peripheral 3, UGAMNH1796; left peripheral 5, UGAMNH1775; left peripheral 8, UGAMNH1835, 1836, right peripheral 9, UGAMNH1779, 1793; left peripheral 10, UGAMNH1767, 1820, 1839; right peripheral 11, UGAMNH1781, 1843; left peripheral 11, UGAMNH1762, 1803-1805, 1816, 1825, 1832, 1845; peripheral, UGAMNH1785, 1824, 1829; left pleural 1, UGAMNH1807; right pleural 2, UGAMNH1799; left pleural 2, UGAMNH1800; left pleural 4, UGAMNH1788; pleural, UGAMNH1771, 1772, 1786, 1808-1815, 1821, 1822, 1838; pygal, UGAMNH1795, 1797, 1818, 1830.

Remarks—This material has the distinctive sculpted appearance of Pleistocene *Trachemys scripta*. All the material is well mineralized. It occurs in freshwater ponds, streams, and rivers (Conant 1975).

Terrapene carolina (Linnaeus)

Eastern Box Turtle

Material—Right and left epiplastron, UGAMNH1703; left hypoplastron, UGAMNH2144; left and right hypoplastron and xiphiplastron, UGAMNH1697, 1698; right hypoplastron at hinge, UGAMNH1686, 1727; left hypoplastron at hinge, UGAMNH1685, 1687, 1690, 1705, 1731; right hypoplastron at inguinal notch, UGAMNH1713; right hypoplastron, UGAMNH1714; left and right hypoplastron, UGAMNH1696, 1715; hypoplastron, UGAMNH1716; neural 1, pleural and peripheral 1 and 2, UGAMNH1699; neural 1 and left and right peripheral 1, UGAMNH1732; neural 5 and 6, UGAMNH1730; neural, UGAMNH1707; nuchal, UGAMNH1704, 1725; right peripheral 1 and

2, UGAMNH1728; left peripheral 1 and 2, UGAMNH1726; right peripheral 1, 2 and 3, UGAMNH1692; left peripheral 1, 2, 3 and pleural 1, UGAMNH1720; left peripheral 3, UGAMNH1722; left peripheral 3 and 4, UGAMNHA1721; right peripheral 3 and 4, UGAMNH1708; right peripheral 5, UGAMNH1688, 1706; left peripheral 5, UGAMNH1691; right peripheral 6 and 7 and pleural 4 and 5, UGAMNH1710; right peripheral 6, 7, and 8, UGAMNH1712; left peripheral 7, UGAMNH1684; left peripheral 8, UGAMNH1702; left peripheral 8, 9, and 10, UGAMNH1694; right peripheral 9, 10, and 11, UGAMNH1733; left peripheral 10, UGAMNH1689; right peripheral 10 and 11, UGAMNH1695, UGAMNH1718; left peripheral 10 and 11, UGAMNH1719, 1734; right peripheral 10 and 11 and pygal, UGAMNH1711; left peripheral 11, UGAMNH1701; left peripheral 11 and pygal, UGAMNH1709; left and right peripheral 11 and pygal, UGAMNH1717; right peripheral 11, UGAMNH1724; left pleural 2 and peripheral 4 and 5, UGAMNH1700; pygal, UGAMNH1683, UGAMNH1723; left xiphiplastron, UGAMNH1327, 1729; left and right xiphiplastron, UGAMNH1693.

Remarks—*Terrapene carolina* can be distinguished from its extinct relative *T. carolina putnami* based on smaller size. It is a terrestrial woodland species (Conant 1975).

Terrapene carolina putnami Hay
Giant Box Turtle

Material—Right epiplastron, UGAMNH1860; left hypoplastron at inguinal notch, UGAMNH1855; left hypoplastron and epiplastron and entoplastron, UGAMNH1863; right hypoplastron and xiphiplastron, UGAMNH1864; neural 1 and pleural and peripheral 1, UGAMNH1856; nuchal, UGAMNH1865; left peripheral 3 and 4, UGAMNH1858; right peripheral 6 and 7, UGAMNH1859; right peripheral 10 and 11 and pygal, UGAMNH1862; right peripheral 1, UGAMNH1849; left peripheral 2, 3, and 4, UGAMNH1848; left peripheral 4, 5, and 6, UGAMNH1861; right peripheral 6, UGAMNH185; left peripheral 7 and 8, UGAMNH1852; left peripheral 8 and 9, UGAMNH1853; right peripheral 9, UGAMNH1847; left peripheral 10 and 11, UGAMNH1854; left pleural 2 and 3 and peripheral 4 and 5, UGAMNH1857; right pleural 2 and 3, UGAMNH1850.

Remarks—This extinct giant subspecies is common in late Pleistocene deposits of Florida where it occurred in coastal marshes and lowland savannahs. (Auffenberg 1958, Kurtén and Anderson 1980). It is readily distinguishable on the basis of its large size.

Family Testudinidae

Testudinidae gen. et sp. indet.

Material—Osteoderms, UGAMNH1645, UGAMNH1646.

Remarks—These specimens represent a large tortoise, but the osteoderms are not diagnostic.

Geochelone sp. indet.

Material—Pleural, UGAMNH1638; left hypoplastron, UGAMNH1639; right pleural 2, UGAMNH1640; left pleural 4, UGAMNH1641.

Remarks—The available material, while certainly *Geochelone*, could not be referred to a species with confidence.

Geochelone incisa (Hay)

Material—Right peripheral 7, UGAMNH1642; nuchal UGAMNH1643; right peripheral 5, UGAMNH1644.

Remarks—This material compares well with the series of *G. incisa* in the collections of the Florida Museum of Natural History and corresponds to Auffenberg's (1963) description. The was apparently an open grassland inhabitant thought to require a frost free winter (Kurtén and Anderson 1980); however, Martin and Guilday (1967) disagree.

Gopherus polyphemus (Daudin)

Gopher Tortoise

Material—Nuchal, UGAMNH1637.

Remarks—This material compares well with modern *Gopherus polyphemus* which ranges in dry sandy soils (Conant 1975).

Family Trionychidae

Trionyx sp. indet.

Material—Carapacial fragment, UGAMNH1761.

Remarks—The available material, while certainly *Trionyx* because of the distinctive pattern on the bone, could not be referred to a species with confidence.

Order Squamata

Family Colubridae

Colubridae gen. et spec. indet.

Material—Vertebrae, UGAMNH2054-2061.

Elaphe obsoleta (Say)

Rat Snake

Material—Vertebra, UGAMNH2055.

Remarks—This material compares well with modern *Elaphe obsoleta* which may be found in woodlands and grasslands (Conant 1975).

Order Crocodilia

Family Alligatoridae

Alligator mississippiensis (Daudin)

American Alligator

Material—Left angular, UGAMNH1015; distal phalanx, UGAMNH1001, right dentary (without teeth), UGAMNH1012; dermal scutes, UGAMNH1003-1011 (1010 and 1011 exhibit crossmends), UGAMNH1023; right femur, UGAMNH1020, 1022; left humerus, UGAMNH1019; fused parietals, UGAMNH1025; left scapula, UGAMNH1014; right scapula, UGAMNH1016, 1018; teeth, UGAMNH1002, 1024, 1026, 1028, 1029; vertebra, UGAMNH1017; frontal, UGAMNH1013; left jugal, UGAMNH1021.

Remarks—This material has the distinctive *Alligator mississippiensis* morphology and it compares well with modern examples. Alligators occur in both fresh and brackish waters (Conant 1975).

CLASS AMPHIBIA

Order Caudata

Family Sirenidae

Siren sp. indet.

Material—Vertebrae, UGAMNH2129-2131, 2161.

Remarks—The available material compares well with modern *Siren*.

Order Anura

Anura gen. et sp. indet.

Material—Vertebrae, UGAMNH2132-2134-right humerii.

Remarks—The available material, while certainly frog, could not be referred to a genus or species with confidence.

CLASS OSTEICHTHYES

Order Lepisosteiformes

Family Lepisosteidae

Lepisosteus sp. indet.

Material—Scales, UGAMNH2109-2111.

Remarks—The scales, while certainly *Lepisosteus*, could not be referred to a species with confidence. *Lepisosteus* occurs in freshwater and estuarine habitats (Hoesé and Moore 1977, Lee et al. 1980).

Order Amiiformes
Family Amiidae
Amia calva Linnaeus
Bowfin

Material—Left dentary, UGAMNH2088; left frontal, UGAMNH2089; cervical vertebra, UGAMNH2090.

Remarks—This material compares well with modern specimens of *Amia calva*. The bowfin is a freshwater and estuarine species (Hoesé and Moore 1977, Lee et al. 1980).

Order Siluriformes
Family Ictaluridae
Ictaluridae gen. et sp. indet.

Material—Spine, UGAMNH2112; vertebra, UGAMNH2113.

Remarks—The available material, while certainly catfish, could not be referred to a genus or species with confidence.

Pylodictis cf. *P. olivaris* (Rafinesque)
Flathead Catfish

Material—Left proximal coracoid, UGAMNH2119.

Remarks—The morphology of the single element is very similar to modern specimens of *P. olivaris* and distinct from the other known regional ictalurids available for comparison. The specimen at hand shows some evidence of mineralization, but mineralization is not extensive. The species occurrence in the St. Marks River is outside its reported range which extends from northeastern Mexico east throughout Gulf of Mexico drainages to Mobile Bay (Lee et al. 1980 et seq.). However, in recent times the species has undergone introductions and populations are now known from at least the Appalachian-Chatahoochee System (M. and B. J. Freeman, University of Georgia, personal communication). Uyeno and Miller (1962) reported some specimens of *P. olivaris* from the Trinity River Terrace, Texas. The deposit was dated to the Sangamon (late Pleistocene); however, that site is within the present range of the species. It is a freshwater species (Hoesé and Moore 1977, Lee et al. 1980).

Family Ariidae
Ariidae gen. et sp. indet.

Material—Spine, UGAMNH2114-2116; cervical vertebrae, UGAMNH2117, UGAMNH2118.

Remarks—These specimens show the characters of the marine catfishes, although species identification is not possible.

Arius felis (Linnaeus)
Hardhead Catfish

Material—Spine, UGAMNH2091.

Remarks—This spine compares well with the distinctive *Arius felis* morphology. This species is restricted to saltwater and estuaries (Hoese and Moore 1977, Lee et al. 1980).

Order Salmoniformes
Family Esocidae
Esox sp. indet.

Material—Right dentary, UGAMNH2101, left dentary UGAMNH2095, 2096, 2098-2100, 2102-2105; dentary, UGAMNH2097; parasphenoid, UGAMNH2106; pharyngeal grinding plates, UGAMNH2107, 2108.

Remarks—These specimens closely resemble both *E. americanus* Gmelin and *E. niger* Lesueur. Both are considered freshwater species (Lee et al. 1980 et seq.) and occur in regional waters today.

Order Perciformes
Family Percichthyidae
Morone saxatilis (Walbaum)
Striped Bass

Material—Right maxilla, UGAMNH2082; right premaxilla, UGAMNH2083; right quadrate, UGAMNH2084, 2085; left quadrate, UGAMNH2086; atlas, UGAMNH2087.

Remarks—This material compares well with modern examples of *Morone saxatilis* which occurs in both coastal saltwater and estuaries (Hoese and Moore 1977, Lee et al. 1980).

Family Sparidae
Archosargus probatocephalus (Walbaum)
Sheepshead

Material—Right dentary, UGAMNH2079; left preoperculum, UGAMNH2080; tooth, UGAMNH2081.

Remarks—This material compares well with modern examples of

Archosargus probatocephalus. The sheepshead is a coastal salt-water and estuary species (Hoese and Moore 1977, Lee et al. 1980).

Family Sciaenidae

Sciaenops ocellatus (Linnaeus)

Red Drum

Material—Quadrate, UGAMNH2092.

Remarks—This material compares well with modern examples of *Sciaenops ocellatus*. It is a coastal saltwater species, but is also associated with estuaries (Hoese and Moore 1977, Lee et al. 1980).

Family Mugilidae

Mugil sp. indet.

Material—Vertebrae, UGAMNH2093, UGAMNH2094.

Remarks—The available material, while certainly *Mugil*, could not be referred to a species with confidence. *Mugil* is a coastal saltwater species (Hoese and Moore 1977, Lee et al. 1980).

RESULTS AND DISCUSSION

CHRONOLOGY AND ENVIRONMENT OF DEPOSITION

Of several thousand separate skeletal elements recovered from the St. Marks River, 1,162 were referable to specific taxa. Included are 37 species of mammals, 3 birds, 13 reptiles, 2 amphibians, and 9 fish. An additional 23 species of birds were identified from the 1972 collection made by Storrs Olson. Of all species we reported, 14 mammals and 2 reptiles are restricted to the Pleistocene. The remaining are representative of the modern extant regional fauna. With the exception of modern contaminants, the latter are acceptable Pleistocene species; however, they more probably represent a mixture of Holocene and Pleistocene material. This is reflected in the range of mineralization observed in many species. In all cases those species known only from the Pleistocene are well mineralized. However, several species with both a Pleistocene and Recent occurrence such as horse and deer exhibit both well mineralized and, what appears to be, very recent unmineralized condition. Modern contaminants such as cow and pig are unmineralized. In general, mineralization is no criterion of Pleistocene deposition. The problem of apparent heterochronous deposition and separation of Pleistocene and Holocene materials is exacerbated by the apparent rapid mineralization that can occur in reducing environments. Neill (1957) noted that rapid mineralization of organic remains in Florida creates the illusion that Recent material is of older age. Nonetheless, the St. Marks River

fauna is clearly mixed and reflects heterochronous deposition over time beginning no later than the late Pleistocene (Wisconsinan) and extending through the Recent.

We compared the St. Marks River faunal list and a modern regional faunal list of the Apalachicola River system (Means 1976). Of the 344 species listed by Means, 29% of the mammals, 10% of the birds, 19% of the reptiles, 5% of the amphibians, and 2% of the fish are represented in the St. Marks River fauna. This bias toward mammals probably reflects taphonomic factors associated with the larger size of mammalian elements in a fluvial environment. Small, more fragile vertebrates (birds, reptiles, amphibians, and fish) are clearly under-represented in the St. Marks River fauna. This bias is reflected also in the mammalian fauna where chiropteran, insectivoran, and small rodent remains are conspicuously absent.

While many of the species recovered from the St. Marks River are eurytopic and provide only limited information regarding the environment of deposition, a number are stenotopic and are considered good environmental indicators.

Mammals—The mammalian fauna, in particular, is very useful in assessing the chronology and paleoenvironment of the St. Marks River. The reason for this is two-fold. First, mammals are the most numerous and have the largest component of extinct forms. Second, Florida has an extremely rich and well-documented late Pleistocene as well as modern mammalian fauna upon which comparisons to the St. Marks River fauna can be made.

Thirteen (35%) of the mammalian fauna of the St. Marks River is represented by extinct forms. These include *Holmsina septentrionalis*, *Megalonyx jeffersonii*, *Glossotherium harlani*, *Canis dirus*, *Smilodon* sp., *Synaptomys australis*, *Tapirus*, sp., *Equus* sp., *Platygonus compressus*, *Hemiauchenia macrocephala*, *Paleolama mirifica*, *Mammut americanum*, and *Mammuthus jeffersonii*. This closely approximates the relative percentage of extinct mammals from a number of Rancholabrean faunas from elsewhere in Florida (Martin and Webb 1974). The temporal span of the extinct forms ranges from Blancan through Recent. However, they all share a late Wisconsinan chronology. Those species representing extant forms, although individually some exhibit a longer stratigraphic history, also share a late Wisconsinan chronology. With few exceptions, all the extant species are represented in the local fauna today.

Comparison of the known and inferred habitat preferences or requirements of the extant and extinct mammalian species suggests the depositional environment was heterogeneous. On one hand there are a number of essentially woodland species: *Didelphis*, *Holmsina*,

Megalonyx, *Lutra*, *Mephitis*, *Urocyon*, *Ursus*, *Tapirus*, *Platygonus*, *Odocoileus*, and *Mammut*. However, grassland species are well represented also: *Glossotherium*, *Mephitis*, *Geomys*, *Equus*, *Hemiauchenia*, *Paleolama*, *Bison*, and *Mammuthus*. From a simple listing it might appear that grassland species are about as common as woodland species. However, when compared by the number of identified specimens per taxon, woodland species are more prevalent. Despite criticism, this method is reliable for a comparison of relative abundances of species (Grayson 1984). In addition, a number of species indicate proximity of water: *Didelphis*, *Lutra*, *Procyon*, *Ursus*, *Castor*, *Neofiber*, *Ondatra*, *Synaptomys*, and *Tapirus* are all typically associated with moist, riparian, or standing water habitats.

Birds—Storrs Olson's collection from the St. Marks River have never been published. He was kind enough to provide a list of the birds identified and has permitted us to include it in the present discussion. Olson (personal communication) felt that "there was very little of interest among the birds" mainly because the list of avian species recovered from the St. Marks River is essentially similar to the modern fauna (Means 1976). As a whole, birds are uninformative concerning the dating of the St. Marks River fauna. They do, however, provide considerable information relating to the environment of deposition.

The St. Marks River avian fauna is clearly biased toward large species with predominantly salt and freshwater marshland habitat preferences: *Podiceps*, *Podilymbus*, *Phalacrocorax*, *Ardea*, *Butorides*, *Egretta*, *Eudocimus*, *Aix*, *Anas*, *Aythya*, *Branta*, *Bucephala*, *Lophodytes*, *Padion*, *Fulica*, *Gallinula*, and *Aramus*. In addition, a number of the species are typically associated with woodlands or woodland riparian habitats: *Aix*, *Mergus*, *Buteo*, and *Strix*. Conspicuously absent are the passeriforms. This probably represents the taphonomic bias referred to above. While a significant number of the birds are often present in saltwater marsh habitats, there are no shorebird (charadriiform) species present.

Reptiles and Amphibians—Many turtles, but few other reptiles, are reported from the St. Marks River. Emydid turtles, in particular, are well represented and make up approximately 90% of the recovered reptilian material. In fact, in numbers alone they make up well over one third the individual elements in the fauna. The emydid turtle species identified from the 1987 collection were *Pseudemys concinna*, *P. floridanus*, *P. nelsoni*, *Trachemys scripta*, and *Terrapene carolina*, all of which are found in the area today. *Pseudemys* and *Trachemys* are indicative of a freshwater environment, while *Terrapene* is terrestrial. An extinct, large, late Pleistocene subspecies of *Terrapene*

carolina, *T. c. putnami*, is represented in the St. Marks River fauna by a number of elements. It was probably limited to the Coastal Plain and Savannah habitats (Auffenberg 1958) and is represented in many late Pleistocene sites in Florida. Other aquatic turtles recovered include one chelydrid, *C. serpentina*, and a number of unreferrable kinosternid fragments. Terrestrial testudinoid turtles present at the site are *Geochelone incisa*, *Geochelone* sp., and *Gopherus polyphemus*. *Geochelone incisa* represents a definite late Pleistocene species, as does *Terrapene carolina putnami*. *Gopherus polyphemus* occurs in the area today.

Only two snakes, *Nerodia* sp. and *Elaphe obsoleta*, were identified from the 1987 collection. Both snakes occur in the area today. No lizards were identified from any of the fossil collections. Two amphibians were recovered, one caudate and one anuran, neither of which could be identified to species.

With the exception of the two late Pleistocene components, the herpetofauna is representative of the modern regional fauna and includes both lower Coastal Plain riverine and marshland species, as well as terrestrial forms.

Fishes—The fish fauna described includes both freshwater and marine forms. *Ariopsis felis*, *Morone saxatilis*, *Archosargus probatocephalus*, *Sciaenops ocellata*, and *Mugil* sp. although typically marine are also estuarine tolerant. The freshwater fishes include *Pyloodictis* cf. *P. olivaris*, *Lepisosteus* sp., *Esox* sp., and *Amia calva*. Of these, *Lepisosteus* sp., *Esox* sp., and *A. calva* tolerate estuarine, but not marine, conditions (Hoese and Moore 1977).

In conclusion, the aquatic community suggests a mixed freshwater and marine, or more likely an estuarine environment, similar to the lower half of the St. Marks River drainage today. The terrestrial fauna indicates a wooded riparian environment also similar to that found in the St. Marks River drainage today. However, the presence of *Hemiauchenia*, *Bison*, *Equus* sp., and *Mammuthus* coupled with *Geomys*, *Geochelone*, and *Gopherus* suggests that more open, semi-forested savannah habitats were also represented. This is consistent with other late Pleistocene (Rancholabrean) faunas from the panhandle of Florida, some of which are considered below.

FAUNAL COMPARISON

The Chipola River sites (IA and IIA)—This is a river deposit similar to the St. Marks River and contains similar species including *Didelphis virginiana*, *Holmesina septentrionalis*, *Castor canadensis*, *Procyon lotor*, *Bison* sp., *Equus* sp., *Mammut americanum*, *Odocoileus virginianus*, and *Hemiauchenia macrocephala* (Webb

1974a). Although no formal paleontological description of the site exists, the species present in that assemblage indicate a mixed woodland/grassland environment (Webb 1974a).

The Aucilla River IA site—The site is also similar to the St. Marks River in depositional and temporal characters. No published paleontological description exists for this site either, but from the fauna a habitat of woodland and marsh can be assumed. It includes *Didelphis virginiana*, *Holmesina septentrionalis*, *Glossotherium* cf. *G. harlani*, *Ondatra zibethicus*, *Castor canadensis*, *Neochoerus pinckneyi*, *Sylvilagus floridanus*, *Canis dirus*, and *Tremarctos floridanus* (Webb 1974a).

Wakulla Springs—This, too, is similar to the St. Marks River in depositional and temporal characters. Included are *Mammuthus* sp., *Mammut americanum*, and *Bison bison antiquus* (Webb 1974a). No formal paleontological description of the site exists.

Generally there are only slight differences between the St. Marks River and other Florida panhandle, riverine deposits. These differences can probably be attributed to a number of causes including collection by amateurs, undersampling, taphonomic events, or other collecting biases.

Compared to the other Rancholabrean faunas from peninsular Florida (Martin and Webb 1974, Webb 1974a, Webb and Wilkins 1984), the St. Marks River assemblage probably is not representative of the full late Pleistocene fauna that existed in the area. For example, more than 50 species of mammals are known to have been present in Florida during the time of accumulation of the Ichetucknee River fauna, Columbia County, Florida (Martin and Webb 1974). As shown by Martin and Webb (1974) mammalian faunal diversity was considerably elevated in peninsular Florida during Rancholabrean time, and it is highly likely that is was the case along the rich fluvio-estuarine environment of the panhandle during the same period.

ACKNOWLEDGMENTS—Thanks are due Chris McKensie, Locke Rogers, Brad Newsom, Tim Gaudin, and Luis Insignares for their efforts below and above the surface of the St. Marks River. Chris McKensie deserves added thanks for the many long hours he spent screening and sorting bones. The United States Department of Agriculture provided an advance copy of their publication on the soils of Wakulla County. Gary Morgan and Russ McArty at the Florida Museum of Natural History were more than just helpful. The gracious offer of Storrs Olson to make available his unpublished records of the avian material he collected and analyzed is greatly appreciated. Robert Martin, Robert Frey, and Elizabeth Reitz provided

many helpful critical comments on earlier drafts. Funds for this study were provided through Department of Zoology and the Museum of Natural History, the University of Georgia.

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No Decline in Salamander (Amphibia: Caudata) Populations: A Twenty-Year Study in the Southern Appalachians

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ABSTRACT—Identical observations, conducted 1-4 times per year for 15-20 years at two locations in the southern Appalachians, have yielded quantitative data on populations of six species of salamanders. Although the numbers have fluctuated for various reasons, there has been no trend in the numbers of any of the species. The "world-wide decline of amphibian populations" has not occurred in the two localities studied.

Recently, much attention has been given to a decline in many populations of amphibians (Barringer 1990, Blaustein and Wake 1990, Phillips 1990). There is a suggestion by some authors that there is a general cause for a supposed "world-wide" decline. We do not deny that many amphibian species have decreased in abundance. Among the causes that have been suggested are acid precipitation (Harte and Hoffman 1989, Beebee et al. 1990) and ultraviolet increase due to ozone depletion (Barringer 1990, Blaustein and Wake 1990, Phillips 1990). The same authors have considered overcollecting and rejected it as a general cause. Habitat destruction is also widely mentioned. The last cause is common to all species, except for some pioneering ones, and would not apply only to amphibians. The situation is regarded by many herpetologists as very serious, so much so that the World Conservation Union (IUCN), Species Survival Commission, has activated a Declining Amphibian Populations Task Force. This group has established local subgroups throughout the United States and elsewhere in the Americas to promote research on the problem.

If there has been a general cause for the decline in amphibian populations, all amphibian populations should be involved; if they are not, the original claim of a "world-wide decline" must be modified, either by eliminating some taxonomic groups, some ecologically distinctive species (e.g., those lacking aquatic stages), or some geographic regions. Study of apparently exceptional cases might give clues to the causes of declines that have been observed.

METHODS

In September 1971 and 1972 N.G.H. and classes from the University of Michigan studied the distribution of the colors of

Plethodon hybrids along altitudinal transects at the Coweeta Hydrologic Laboratory, near Franklin, North Carolina, and in 1972 they also recorded the ecological distribution of four species of *Desmognathus* (Hairston 1973). In 1973 and 1974, N.G.H. studied a zone of intergradation between two forms of *Plethodon jordani* and the altitudinal replacement of that species and *P. glutinosus* at Heintooga Overlook in the Great Smoky Mountains National Park near the junction of the Balsam Mountains and the Great Smoky Mountains in Haywood and Swain counties, North Carolina. The name *glutinosus* is controversial for this form; Highton (1983) proposed the name *teyahalee*, which we believe to be misapplied (Hairston 1992).

N.G.H. also continued the observation of *Plethodon* hybrids at Coweeta in 1974. Beginning in September 1976 and for each year thereafter, we have led one to four (usually two) undergraduate classes of 15 students each to both localities and made carefully repeated observations of the same kind.

At Heintooga, the students were instructed to capture 10 *Plethodon*, return with them to the vehicles, and examine the animals' cheeks for the amount of red color; specimens were then returned to the forest. The exercise was repeated at 3.2, 6.4, 9.7, 11.3, and 13.7 km along the National Park Service road to Round Bottom Camp Ground, with species identifications made at the last two stops. The elevations ranged from 1,600 m at the start to 1,350 m at the last stop. At Coweeta, the same exercise was carried out at five elevations, starting at 686 m and continuing up at 91.5-m intervals. We and the students evaluated the amount of red on legs and the amount of white on sides and back. Both of these exercises were performed at night, beginning at dark. The *Desmognathus* exercise involved the students collecting specimens and noting identification of each and the distance from nearest surface water to where they were found. The exercise requires a period of 2-2.5 hours in the afternoon.

Each class exercise on *Plethodon* began at dark (2000 hours) and ended at approximately the same time each night (2330 hours at Heintooga and 2230 hours at Coweeta). The *Desmognathus* exercise began at 1230 hours and ended at approximately 1430-1500 hours. Thus, there has been no tendency to expend extra effort to observe the same number of salamanders.

RESULTS

There has been no consistent trend in the number of individuals of any of the seven populations over the 15-20 years of the study (Figs. 1-3). All seven series show fluctuations greater than more exact studies showed over shorter periods near the sites reported here

(Hairston 1987). There are several known causes for the fluctuations, which occurred over much shorter intervals than the mean generation times (5-10 years) for the different species (Hairston 1987). Some were due to cold weather, when *Plethodon* tend to remain underground (first class, September 1981); others were due to exceptionally enthusiastic classes (September 1977). None of the fluctuations in numbers observed can be attributed to a real change in the number of salamanders actually present. The mean generation time for *P. jordani* is 9.8 years and for *glutinosus* it is at least a year longer (Hairston 1987). Thus, fluctuations in numbers seen at shorter intervals do not represent real changes.

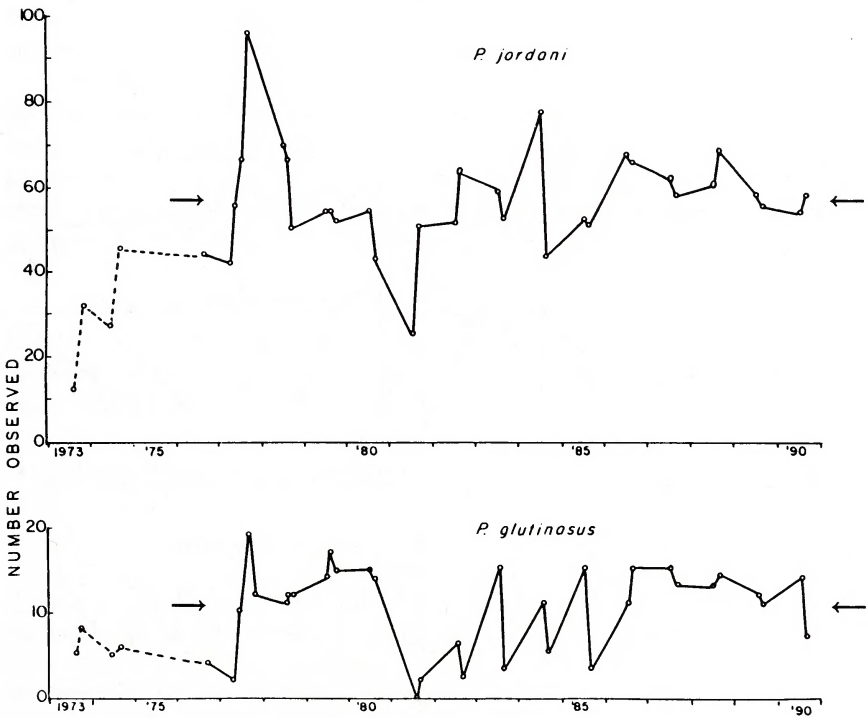


Fig. 1. Population history of *Plethodon jordani* and *P. glutinosus* in the Heintooga locality, as shown in numbers observed by successive classes from 1976 to 1990. Broken lines represent preliminary observations not exactly equivalent to class date. Arrows show means of all class data; standard error not given because the counts might not be independent because of the longevity of individual salamanders and the likelihood that at least some of the same ones were observed on successive class exercises.

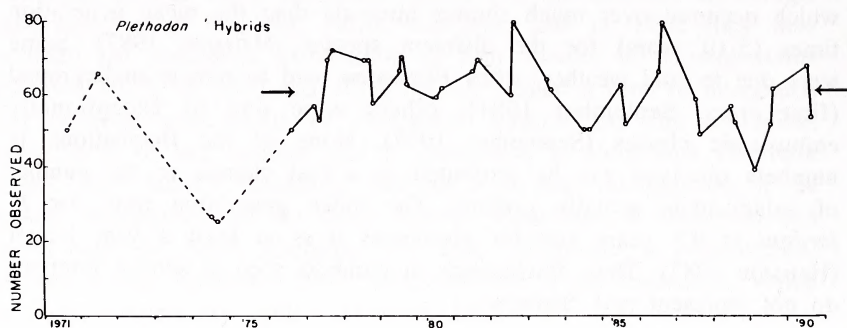


Fig. 2. History of the *Plethodon* population at Coweeta. Symbols are the same as in Figure 1.

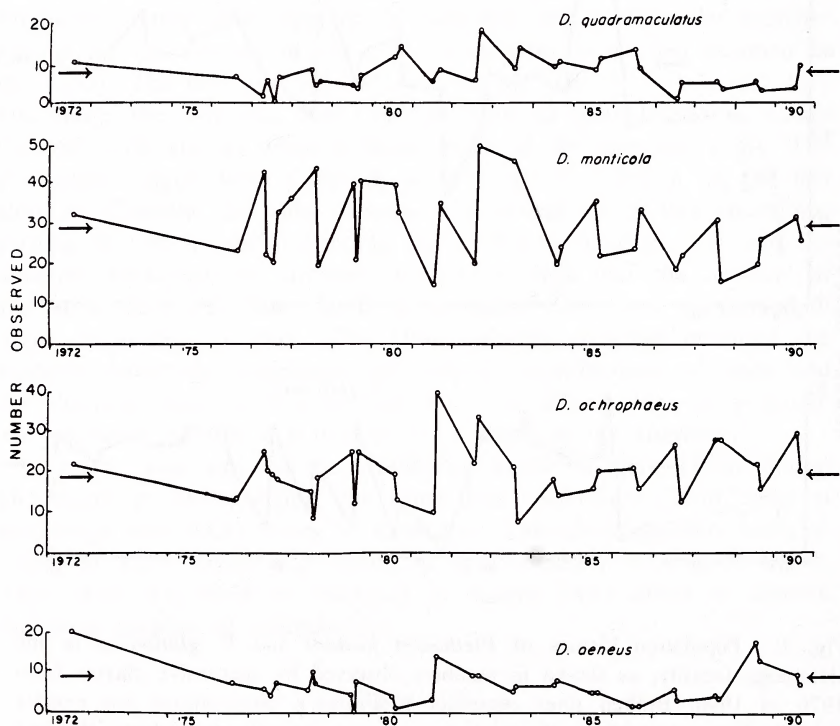


Fig. 3. Population histories of four species of *Desmognathus* at 686-m elevation, Coweeta Hydrological Laboratory. Symbols are the same as in Figure 1.

DISCUSSION

As far as we know, this is the longest series of continuous quantitative observations on any amphibian populations. Other multiple-year studies include 13 years for Savannah River Ecology Laboratory studies (Pechmann et al. 1991) and the same duration for *Taricha rivularis* in California (Twitty 1966). In the former, changes could be explained by drought, and the latter was completed long before the supposed general decline of amphibian populations.

Our observations bear on some of the suggested causes for long-term declines in amphibian populations. There is considerable evidence that the observed dieback and decline of spruce-fir forests in the southern Appalachians is due to atmospheric pollution (Bruck 1988, Dall et al. 1988, Zedaker et al. 1988). As the salamander populations have remained essentially in steady states, acid rain and ozone depletion cannot be universal causes of all declines in amphibian populations.

As the great majority of records of population declines are based on anecdotal evidence, we remain skeptical of the generality of these declines until similar long-term records are produced. We are also convinced that over-collecting by biological supply companies and by some herpetologists has been underrated as a possible cause of observed declines.

ACKNOWLEDGMENTS—We thank successive officials of the Great Smoky Mountains National Park for permission to carry out the study at Heintooga. We also thank Wayne Swank, Director, Coweeta Hydrologic Laboratory for permission to carry out the studies there. Without the dedicated efforts of the hundreds of students in our classes, as well as those of the teaching assistants, the data could not have been collected.

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Accepted 7 August 1992

On the Validity of the Name *teyahalee* as Applied to a Member
of the *Plethodon glutinosus* Complex
(Caudata: Plethodontidae): A New Name

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ABSTRACT—The name *Plethodon teyahalee* (Hairston) cannot be applied to the member of the *P. glutinosus* complex as designated by Highton (1983). Biochemical data show that the population from which the type of *teyahalee* was taken consists of hybrids between local populations representing the *P. jordani* and *P. glutinosus* complexes, and thus cannot be applied to a member of either of those two species under Article 23(h) of the International Code of Zoological Nomenclature (1985). A new name, *Plethodon oconaluftee*, is proposed, and a new type is designated.

Plethodon glutinosus, a salamander distributed widely over the eastern United States, has recently been divided into 16 species on the basis of allozyme frequencies (Highton 1983, 1989). Most of these forms occupy non-overlapping distributions, and it is not known at present whether they are allopatric or parapatric. The form that is distributed west of the French Broad River throughout southwestern North Carolina and immediately adjacent parts of Tennessee, Georgia, and South Carolina is one of the few that overlaps any adjoining species of the complex without hybridization. In extreme southeastern Tennessee and extreme southwestern North Carolina, it overlaps *P. aureolus* and *P. glutinosus* (sensu stricto). Highton (loc. cit.) has appropriated the name *teyahalee* for this representative of the *glutinosus* complex.

In 1950 I described a form from Teyahalee Bald in the Snowbird Mountains of southwestern North Carolina as *P. jordani teyahalee*, believing it to be closely related to other subspecies of *P. jordani* (Hairston 1950). The presence of red spots on the legs of some individuals indicated the population's relationship to *P. j. shermani* of the Nantahala Mountains, and the greenish-yellow spots on the sides appeared to make it unique. Subsequent collectors have failed to find any specimens with the greenish-yellow spots, and Highton (1962), in a review of the genus, argued that they could be explained as follows: "Sometimes the lateral pigment of large specimens (of *glutinosus*) is more yellowish than in small ones, but structurally the pigment appears the same." He did not comment on the detailed differences between the white spots of *P. glutinosus* and those of

some populations of *P. jordani* figured by Hairston and Pope (1948). His conclusion was that only a representative of *glutinosus* is present on Teyahalee Bald and that it has genetically swamped a pre-existing form of *jordani* (Highton and Henry 1970); Highton 1972, 1989), using that as his justification for appropriating the name *teyahalee*.

We have known for more than 50 years that the high-altitude red-legged form of *P. jordani* and the low-altitude white-spotted form then known as *glutinosus* are hybridizing at intermediate elevations throughout the Nantahala Mountains, a short distance from Teyahalee Bald (Bishop 1941, Highton and Henry 1970). As the hybrid zone in the Nantahala Mountains is spreading toward higher elevations (Hairston et al. 1992), Highton's interpretation appears reasonable. More recently, some hybridization has been found at other localities, but not in the area between the Tuckaseegee and French Broad rivers, nor in the western two-thirds of the Great Smoky Mountains, nor in the Cheoah, Max Patch, or Sandy Mush mountains, nor in the southern 95% of the Balsam Mountains, i.e., not in more than half of the distribution of this representative of the *glutinosus* complex.

The important question is the status of the population of *Plethodon* on Teyahalee Bald. Allozyme data presented by Peabody (1978) show that these animals are intermediate between neighboring populations of *jordani* and the low-altitude representative of the *glutinosus* complex. In fact, the calculated values of Nei's Genetic Identity are more similar to the nearest populations of *jordani* than they are to the nearest populations of the *glutinosus* complex (Table 1). The genetic swamping is thus so incomplete that the entire population on Teyahalee Bald must be regarded as hybrids, and judging from the history in the adjacent Nantahala Mountains have been hybrids since at least 1938 (Bishop 1941) and probably earlier (Hairston et al. 1992).

Table 1. Genetic identities (Nei's I [Nei 1972]) among the Teyahalee Bald population, the nearest populations of the *Plethodon glutinosus* complex, and the nearest populations of the *P. jordani* complex. Note that both *jordani* and *glutinosus* are represented at Cheoah and Unicoi West. Data from Peabody (1978).

Species Complex					
<i>P. glutinosus</i>			<i>P. jordani</i>		
Location	Distance from Teyahalee (km)	Nei's I	Location	Distance from Teyahalee (km)	Nei's I
Cheoah	11.6	0.963	Cheoah	11.6	0.805
Unicoi West	21.8	0.694	Unicoi East	16.0	0.900
Fontana	24.0	0.941	Wayah	16.5	0.942
			Tusquitee	16.7	0.969
			Unicoi West	21.8	0.920

The situation on Cheoah requires comment. No hybridization occurs there, and the samples of the two species are therefore distinct. That representative of the *P. jordani* complex is more distantly related to the other four populations than they are to each other. The average genetic identity between it and them is 0.857 (range = 0.813–0.895); the average identity among the other four populations is 0.932 (range = 0.900–0.967). The population on Teyahalee Bald is closely related to those four representatives of *P. jordani*, but not to the Cheoah representative.

It appears, therefore, that what I described as *Plethodon jordani teyahalee* was a hybrid, and under Article 23(h) of the International Code of Zoological Nomenclature the name *teyahalee* cannot be used for that part of the *glutinosus* complex to which it was applied by Highton (1983, 1989), because that is one of the parent species. To avoid future confusion I have collected a new type for this form from an area where hybridization with *P. jordani* is unknown, and I propose the name *Plethodon oconaluftee*.

The following synonymic list is taken from Highton (1989): *Plethodon glutinosus* (Green): Brimley (1912) (part), Highton (1970) (part) [actually Highton and Henry (1970)]. *Plethodon jordani teyahalee* Hairston (1950:269). *Plethodon jordani* Blatchley: Highton (1962). *Plethodon (glutinosus) glutinosus* (Green): Bishop (1941) (part). *Plethodon teyahalee* Hairston: Highton (1984) [actually Highton 1983].

Holotype—GSMNP 33339, an adult female collected 16 May 1991, by N. G. Hairston, Sr., Pisgah National Forest, beside Forest Service Road 140 near the North Fork of the French Broad River at an elevation of 930 m on the south-facing slope of the Balsam Mountains, Transylvania County, North Carolina. Snout to posterior angle of vent, 75 mm; numerous very small white spots on back and top of tail, a few on top of head; numerous irregularly shaped white spots on sides and cheeks; underside dark throughout, including throat and chin, which have a number of irregular white spots.

Paratype—GSMNP 33340, an immature female (about 3 years old) collected in same place as the type on 17 May 1991 by M. P. Hairston. Snout to posterior angle of vent, 39 mm; dorsum, sides, head, and cheeks as for type; belly dark, throat and chin paler than in type, with many melanin-free spots, but with white pigment only in a few lateral ones. Both types have been deposited in the collections of the Great Smoky Mountains National Park.

The following diagnosis and distribution are quoted from Highton (1989), which I use because we discuss the same taxonomic entity: "*Diagnosis*: A large, light-chinned species with very small white dorsal

spots, reduced lateral spotting, and often with small red spots on the legs. The unique combination of genetic alleles that distinguishes *P. teyahalee* from other species of the *P. glutinosus* group is Pgi allele *c* and Trf allele *a* are characteristic of *P. teyahalee* populations but are usually rare or absent in the other species." (Highton 1989:54) ("*teyahalee*" used because of the direct quotation).

"*Distribution*: West of the French Broad River in the Blue Ridge physiographic province of southwestern North Carolina and in immediately adjacent Tennessee. It also occurs in northern Rabun County, Georgia, and in Oconee, Pickens, Anderson, and Abbeville counties, South Carolina." (Highton 1989:54).

ACKNOWLEDGMENTS—I thank Richard Highton for a friendly discussion of the issues involved and for suggesting the locality from which the types of *P. oconaluftee* were collected. Three anonymous reviewers made constructive suggestions.

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Accepted 26 March 1992

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Differences in Variation in Egg Size for Several Species of Salamanders (Amphibia: Caudata) That Use Different Larval Environments

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ABSTRACT—Comparative descriptive data are provided on variation of egg size in five species of salamanders. The species differ in their use of larval habitats. *Ambystoma maculatum* uses temporary, rain-filled pools in the southern Appalachian Mountains. *Desmognathus aeneus* is a direct developer and is not constrained by risk of larval desiccation. The remaining three species, *Eurycea wilderae*, *D. ochrophaeus*, and *D. santeetlah*, have permanent streams as their larval environment. Using the coefficient of variation (CV), I document both variation within individual clutches and variation at the interclutch level. The degree of variation differs among individual clutches and among species. Variation at the intraclutch level does not agree with that predicted. However, variation at the interclutch level conforms to the prediction that *A. maculatum* (which utilizes ephemeral larval environments) exhibits the highest degree of variation in egg size.

In many populations of biphasic amphibians, the key factor underlying the timing of metamorphosis and larval survivorship is the time for which the larval environment remains hospitable. In a permanent larval habitat, where mortality from desiccation is unlikely, the larval period of an amphibian can be long. For example, paedomorphic species of salamanders inhabit permanent bodies of water. However, many species of amphibians inhabit larval environments that are temporary and unpredictable, and desiccation is a threat to species that use those bodies of water. Because environmental pressure to escape the larval environment can vary from year to year, species that breed in temporary pools may exhibit different reproductive strategies than species that use permanent bodies of water.

Parental investment, one facet of the study of reproductive strategies, has been the subject of theoretical and/or empirical studies in amphibians (e.g., Wilbur 1977; Kaplan 1980, 1985; Crump 1981, 1984; Kaplan and Cooper 1984). These studies have documented the

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extensive variation in propagule size in amphibians. Such variation has been interpreted as an "evolved tactic" (Capinera 1979) that ensures that viable offspring are produced in variable habitats. In many species of amphibians with complex life cycles, vitellogenesis occurs in the terrestrial habitat. The female then may not be able to receive environmental cues that indicate the size of eggs she should produce to ensure survival of offspring in the aquatic habitat. Because offspring can be exposed to a habitat that is variable, there should be an optimal range in offspring size within an individual female's clutch. As habitat variability decreases, the range should decrease because of consistent selection for an optimal phenotype.

Egg size also varies among clutches. A single female might produce clutches with very different mean egg sizes (Kaplan 1987). Kaplan and Cooper (1984) showed that in species that cannot "predict" the stability of the environment in which their larvae will grow and develop, the most efficient strategy will be to randomly produce a few large eggs or many small eggs. Interclutch variation in egg size in a female's lifetime (or within a population at one time) can outweigh the intraclutch variation of a female's single clutch.

Egg size has been shown to influence characters that relate to larval survival in salamanders (Kaplan 1980, 1985; Petranks 1984). Kaplan (1985) showed that in the newt *Taricha torosa* (Rathke, 1883) egg size can have profound effects on hatching size and growth rate. Thus, egg size might affect timing of metamorphosis. If so, then an optimal egg size can be selected for given a stable (or permanent) larval environment. In an unreliable environment, an optimal range of egg sizes might be the best strategy to maximize parental fitness. In *T. torosa*, large eggs produce large hatchlings that begin feeding sooner than smaller larvae. When fed ad libitum, larger larvae will metamorphose at an earlier time and at a larger size than conspecifics hatched from small eggs. In food-limited situations, larvae from larger eggs still metamorphose at a larger size but at a later time than larvae from small eggs. This interaction among egg size, food availability, and habitat reliability suggests that the optimal egg size can vary from season to season.

I present data on variation in egg size in five species of salamanders. Three questions are explored: (1) Does a species that uses temporary larval environments exhibit greater intraclutch variation in egg size than species that use more permanent larval habitats, such as mountain streams? (2) Is the total population variation in egg size greater in a species that uses temporary larval environments than in species that use mountain streams? (3) Is the

bulk of variation in egg size introduced at the intraclutch or interclutch level, and is this related to habitat variability?

MATERIALS AND METHODS

STUDY SPECIES

Ambystoma maculatum (Shaw, 1802) in the southern Appalachian Mountains usually breeds in mid-winter in temporary, seasonal pools that result primarily from heavy rains. Larvae emerge from eggs in early spring, and metamorphosis occurs 60-120 days later (Bishop 1941, Shoop 1974). The collection sites I used in this study dry completely 1-6 months after the rains, and on occasion they dry too early for any larvae to transform (R. C. Bruce, personal communication). Populations of *A. maculatum* in eastern North America are known to lay one mass of eggs per clutch (Wilbur 1977, Pfingsten and Downs 1989) or two or more masses per clutch (Bishop 1941, Pfingsten and Downs 1989). "Masses" will be referred to as "clusters" in this article. It is unknown if the clutch of a female *A. maculatum* at this locality consists of one or multiple clusters. Eggs of *A. maculatum* were collected in March 1988 from four temporary pools located in Blue Valley on the escarpment of the Blue Ridge Mountains, Macon County, North Carolina.

Eurycea wilderae Dunn, 1920, *Desmognathus santeelah* Tilley, 1981, and *D. ochrophaeus* Cope, 1859 lay eggs in and along headwater streams. These sites represent permanent sources of water, even during seasons of drought (W. Swank, Coweeta Hydrologic Laboratory, personal communication). Fishes are uncommon in these headwater streams. The permanence of these sources of water is evident when one considers that several species of plethodontids have larval periods in excess of 3 years, e.g., *D. quadramaculatus* (Holbrook, 1840) and *Gyrinophilus porphyriticus* (Green, 1827) (Bruce 1980, 1988a). *Eurycea wilderae* has a larval period of 1 or 2 years (Bruce 1988b). Females attach their eggs to the undersides of large rocks where the clutch is exposed to running water. *Eurycea wilderae* clutches were collected during February and March 1988 at Wolf Creek on Cullowhee Mountain, in the Cowee Mountains, Jackson County, North Carolina. Clutches were located by raking through cobble of headwater seepages.

Desmognathus ochrophaeus clutches were collected from various headwater streams in the Balsam Mountains in Haywood and Jackson counties, North Carolina. The Balsams are a southern extension of the Great Smoky Mountains, Swain County, North Carolina where the *D. santeelah* clutches were collected. *Desmognathus santeelah* and *D. ochrophaeus* females brood the eggs under moss on logs and

rocks in and along the edges of headwater streams and seepages. These species of *Desmognathus* have larval periods less than one year (Bruce 1989). Clutches of the *D. ochrophaeus* and *D. santeetlah* were collected during July and August 1987.

Desmognathus aeneus Brown and Bishop, 1947 females oviposit under moist logs and moss. This species is direct-developing (Wake 1966), and desiccation risk should represent less constraint to it. Clutches of *D. aeneus* were collected in the vicinity of Standing Indian Campground in the Nantahala Mountains, Macon County, North Carolina, in May 1988.

COLLECTION OF MATERIAL

As soon as I collected them, I placed egg clutches in individual plastic containers. If I found a brooding female with the clutch, I collected her and placed her with it. The plastic containers were placed in a cooler and returned to the laboratory where the egg clutches were assigned Harrison developmental stages (Duellman and Trueb 1986). I used a dissecting microscope equipped with an ocular micrometer to measure egg diameters to the nearest 0.1 mm. Late developmental stages were assigned based primarily on gill ontogeny. Embryos of clutches in which the embryos were in later stages of development were adjusted for developmental increases in size with the transformation formulas of Kaplan (1979). Clutches of *A. maculatum* and *D. aeneus* were all collected very early in development. The other three species were collected at various developmental stages, some of them at late stages. Embryo diameters for the plethodontid species in late development were recorded as the length of the longest axis of the embryo (Fig. 1). Using this measurement protocol, I observed that plethodontid embryos do not begin to increase in size until after Harrison stage 30 (Beachy 1988).

ANALYSES

Intraclutch variation was quantified by calculating the coefficient of variation (CV) for each clutch. The CV is a statistic that expresses the standard deviation as a percentage of the mean so that groups having very different means can be compared. These intraclutch CVs were subjected to a one-way ANOVA by species. Although a single female of *A. maculatum* may oviposit several clusters of eggs, I assumed that differences among these clusters do not contribute significantly to the variance in CVs, and all *A. maculatum* clusters were treated as though they were from different females (however, see Results).

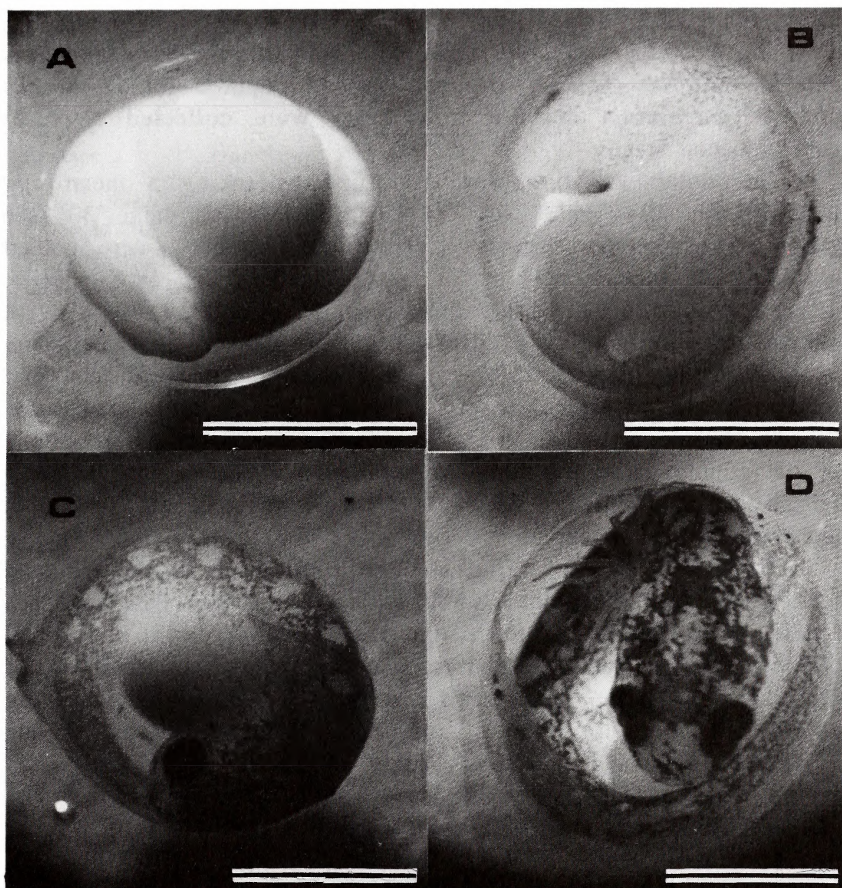


Fig. 1. *Desmognathus santeetlah* embryo at four different Harrison developmental stages: (A) stage 25, (B) stage 35, (C) stage 40, (D) stage 45. Note spherical orientation of embryo, even at late developmental stages. Bars = 2.0 mm.

Egg laying is not synchronous in plethodontid salamanders, and this precludes collection of a large number of plethodontid clutches at early stages of development. Therefore, I collected clutches at various stages of development. To ensure that intraclutch variation did not vary with development, a Wilcoxon's matched-pairs signed-ranks test was conducted on 12 *D. santeetlah* clutches to test if stage of development significantly influenced CV. Coefficients of variation were calculated for two developmental stages (stage 45 and an earlier stage, ranging from 9 to 41 for the clutches in question) for each clutch, and no significant difference was found in CV due

to development (\bar{x} early stage = 5.43, \bar{x} stage 45 = 5.96, $n = 12$, $T_s = 21$, ns). This result was assumed to hold true for *D. ochrophaeus* and *E. wilderae*. This assumption was not required for *D. aeneus* and *A. maculatum* because these eggs were collected at early developmental stages.

Interclutch variation was quantified by taking a mean egg diameter for all clutches at, or prior to, Harrison stage 30 (see above discussion on changes in size). These means were pooled according to species, and a CV was calculated for each species. These species CVs were squared and subjected to pairwise *F*-tests (Lewontin 1966). Kaplan (1987) showed that *Bombina orientalis* (Boulenger, 1890) females can produce clutches of different mean egg sizes. By assuming that this is the case for the species used in my study (i.e., the variation represented in a sample of the population might mirror the variation introduced by a single female in her lifetime), one can set predictions that are similar to those for intraclutch variation.

To determine the relative contributions of intraclutch and interclutch variation to the overall variance, egg size data for each species were subjected to a one-way ANOVA, with individual clutches as the factor. Relative contributions of intraclutch and interclutch variation to overall variance for each species were calculated using the factor and error sum-of-squares of the ANOVA table (Sokal and Rohlf 1981).

I analyzed data with StatView512+TM following the methods of Sokal and Rohlf (1981). In all analyses $\alpha = 0.05$.

RESULTS

My hypothesis was that the variation in egg size would be greatest in *A. maculatum*, the temporary pool breeder, and the lowest in *D. aeneus*, which is not constrained by habitat variability and thus should exhibit the greatest degree of canalization. Variation in egg size should be intermediate in the other three species. Descriptive statistics of egg size for the five species under study are presented in Table 1.

INTRACLUTCH VARIATION

Coefficients of variation of all clutches were analyzed with a model I one-way ANOVA (Sokal and Rohlf 1981), with species as treatment. Significant differences were found in intraclutch CV among species. A Fisher's PLSD a posteriori test was employed to determine the nature of the differences. The prediction that species using ephemeral larval habitats will display larger variation in egg size was not supported. Of all species, *D. aeneus* exhibited the

Table 1. Descriptive statistics of egg size for five species of salamanders.^a

Species	Number of clutches	Clutch size		Egg size (mm)	
		\bar{x}	SD	\bar{x}	SD
<i>A. maculatum</i>	37 ^b	67.24	34.71	3.15	0.40
<i>D. ochrophaeus</i>	6	15.00	3.56	3.32	0.11
<i>D. santeetlah</i>	29	20.01	6.00	3.43	0.25
<i>E. wilderae</i>	6	14.77	4.85	3.26	0.24
<i>D. aeneus</i>	10	11.80	2.23	2.54	0.13

^aData are calculated using mean egg size per clutch. Only data for those clutches at, or earlier than, Harrison developmental stage 30 are presented (see text for explanation).

^bRefers to clusters for *A. maculatum*.

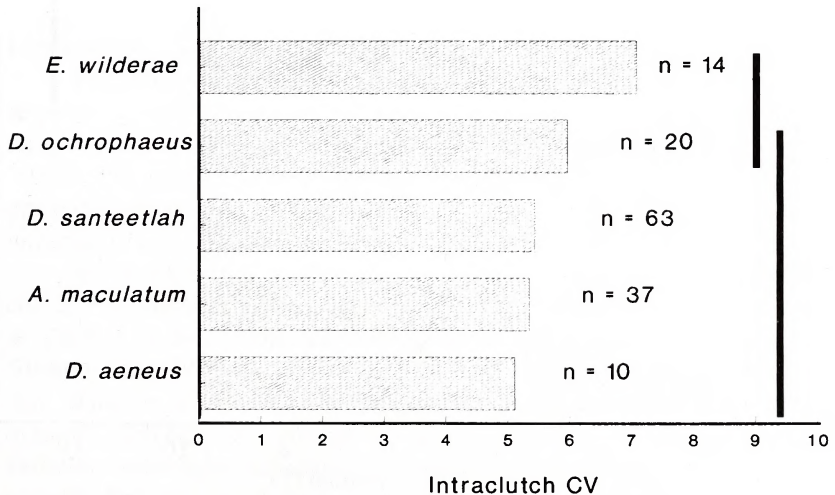


Fig. 2. Coefficients of variation (CV) of intraclutch variation in egg size for five species of salamanders. Number of clutches examined for each species is indicated. Vertical lines indicate means not significantly different using a model I ANOVA with species as treatment. ($\alpha = 0.05$).

lowest degree of variability, as expected. But *A. maculatum* did not exhibit the highest degree of intraclutch variation as was expected (Fig. 2).

INTERCLUTCH VARIATION

Because embryo diameter begins to increase in late developmental stages, only those clutches of *D. santeetlah*, *D. ochrophaeus*, and *E. wilderae* collected earlier than Harrison developmental stage 30 were used in this analysis. All egg size data for *A. maculatum* and *D. aeneus* were analyzed. Mean egg size was determined for each clutch, and those data were used to calculate a CV of egg size for each species (Table 1). In this analysis, *A. maculatum* did show the greatest variation in egg size (Fig. 3). Except for *E. wilderae*, all species CVs were significantly lower than that for *A. maculatum*. *D. aeneus* was predicted to exhibit the lowest degree of variation in egg size; only *D. ochrophaeus* has a lower CV, although this difference was not significant.

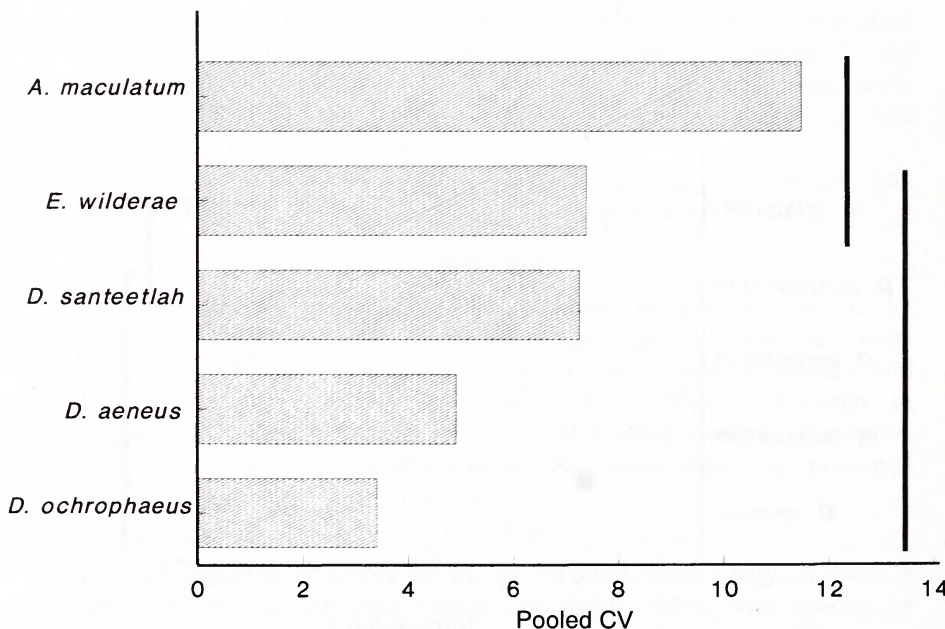


Fig. 3. Coefficients of variation (CV) of pooled (interclutch) variation in egg size for five species of salamanders. The species CVs are tested with an *F*-test of the squared CVs (Lewontin 1966). Vertical lines indicate means not distinguishable by pairwise *F*-tests ($P > 0.05$).

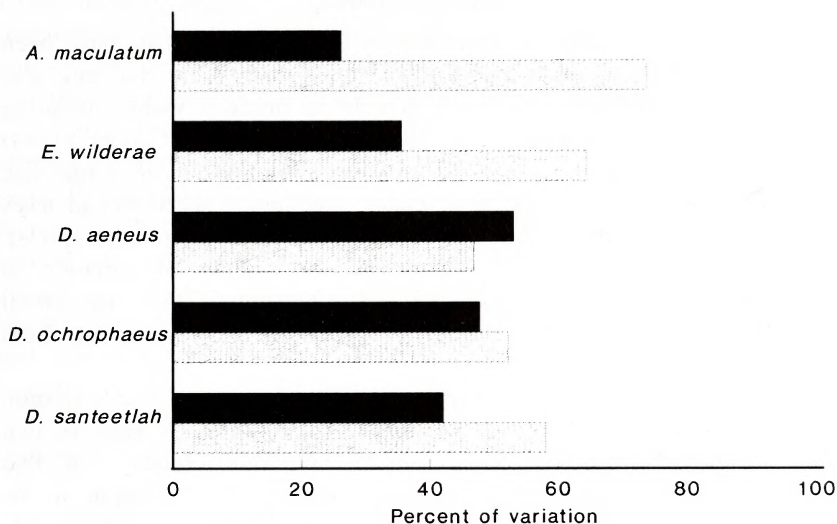


Fig. 4. Relative contributions of intraclutch and interclutch variation in egg size to overall variance. For each species, a separate model II one-way ANOVA of egg size was conducted with clutches as the factor, thus a total of five ANOVAs. Contributions are calculated using the factor and error sum-of-squares of the ANOVA table. Black bars represent intraclutch variation, and hatched bars represent interclutch variation.

INTERCLUTCH AND INTRACLUTCH CONTRIBUTION TO VARIATION

Partitioning of the variance components demonstrated the respective contributions of intraclutch and interclutch variation to the sample variance in egg size (Fig. 4). For *E. wilderae* and *A. maculatum*, interclutch contributions to the variance outweighed intraclutch contributions. In all three desmognathines, interclutch and intraclutch contributions were approximately equal.

As pointed out earlier, *A. maculatum* females may oviposit a clutch that consists of several clusters. The mean cluster size reported in Table 1 is lower than earlier reports of clutch size in *A. maculatum* (Bishop 1941, Wilbur 1977, Pfingsten and Downs 1989). This suggests that females of *A. maculatum* in the southern Appalachians may oviposit clutches that consist of several clusters. Because interclutch variation outweighs intraclutch variation in this species, the possibility remains that several clusters might contribute to a single *A. maculatum* clutch. This may confound the analysis of intraclutch variation, i.e., the intraclutch CVs for *A. maculatum* might be underestimates. However, the pooled variation remains as an indicator of potential adaptive variation in egg size at the interclutch level.

DISCUSSION

The potential role of variation in offspring size has long been a topic of debate. Kaplan and Cooper (1984) suggested that egg size variation in amphibians enables a female to produce viable offspring in unpredictable environments. In addition, Kaplan and Cooper (1984) submit that there are two levels at which variation in offspring size may be introduced: within a single clutch and among successive clutches of an individual female (i.e., at the intraclutch and interclutch levels). I tested these hypotheses by comparing the amount of variation in egg size observed in five species of salamanders that use larval environments ranging (in terms of safety from desiccation) from permanent to ephemeral.

These data add to the existing evidence showing that variation in egg size in amphibians is extensive. In addition, it appears that variation in offspring size differs among individual clutches and that the degree of variation differs among species. The question to be asked is whether the degree of variation is related to different life history strategies employed by species using different environments.

Kaplan and Cooper (1984) proposed that variation in amphibian egg size might reflect different reproductive strategies. In their attempt to model parental investment, they included a consideration of the extensive variation in propagule size seen in amphibians, insects, and plants. Earlier models of parental investment lacked this aspect (e.g., Smith and Fretwell 1974). A study by Crump (1981) emphasized the potential role of variation in amphibian egg sizes. Crump found no significant differences in egg size variation among species of treefrogs that use habitats of differing variability. However, among species that use temporary ponds, individual females produced clutches that tended toward a platykurtic distribution of egg size (bet hedging). Those species that breed in permanent ponds tended toward a leptokurtic distribution (canalization).

However, Crump's evidence has been criticized as unconvincing (McGinley et al. 1987). In a mathematical consideration of Smith and Fretwell's and Kaplan and Cooper's models, McGinley et al. (1987) suggested that variable environments do not necessarily select for variable parental investment in offspring. Parental fitness can be maximized, even in heterogeneous environments, by investing equally in all offspring. Is variation in egg size adaptive? Or are there factors that prevent a female from investing equally in all offspring?

If one were to consider only the intraclutch variation that I present here, the supposition that variation in egg size is correlated with desiccation risk appears to garner little support. The data on interclutch variation, however, suggest that species that use ephemeral

larval habitats might be able to introduce variation in egg size by ovipositing successive clutches with different mean egg sizes. *A. maculatum* did exhibit the largest degree of interclutch variation, and the other species followed in nearly the predicted order.

Smith-Gill (1983) suggested that much adaptive variation can be introduced at the whole organism level through developmental mechanisms, the mechanism in this case being vitellogenesis. Those developmental mechanisms that provide for variation should be subject to natural selection; i.e., those mechanisms should provide the amount of variation that maximizes an individual's fitness. The variation in egg size in the species examined provides some support for the hypothesis that this variation is correlated with habitat variability and is possibly adaptive. It remains to be seen if the hypothesis of adaptive variation in egg size is supported when more species of amphibians are investigated.

ACKNOWLEDGMENTS—This research represents a portion of work submitted in partial fulfillment of the requirements for the M.S. degree at Western Carolina University, Cullowhee, North Carolina. R. C. Bruce, M. L. Crump, R. G. Jaeger, R. H. Kaplan, C. L. Ory, and S. C. Walls reviewed versions of the manuscript. S. G. Tilley kindly identified some of the clutches of *Desmognathus*. I thank J. B. Bernardo, R. C. Bruce, and S. R. Voss for their help in collecting clutches of eggs and for helpful criticisms during the completion of this project. This work was supported by The Highlands Biological Station and Louisiana Board of Regents Doctoral Fellowship LEQSF (1988-1994)-GF-15.

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Helminth Parasites of the Eastern Box Turtle,
Terrapene carolina carolina (L.)
(Testudines: Emydidae), in North Carolina

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ABSTRACT—We examined 117 eastern box turtles, *Terrapene carolina carolina*, for helminth parasites. Nine species (two trematodes, six nematodes, and one acanthocephalan) were recovered, and 39% of the turtles were infected with three–five species of parasites. Infection rates were as follows: *Oswaldocruzia* sp. (82.9%), *Spironoura affinis* (76.1%), *Telorchis robustus* (29.9%), *Cosmocercoides dukae* (20.5%), *Aplectana* sp. (6.0%), *Brachycoelium salamandrae* (2.6%), *Physaloptera* sp. (2.6%), *Serpinema* (= *Camallanus*) *microcephalus* (0.9%), and *Macracanthorhynchus ingens* (0.9%). Ulcerations of the stomach mucosa harbored larval *Spironoura affinis*. The presence of *Spironoura affinis*, *Telorchis robustus*, and *Serpinema microcephalus* suggests a close phylogenetic relationship of *Terrapene* to other emydid turtles. The other helminth species are normally found in amphibians and might represent parasites acquired in the turtle's evolutionary transition from an aquatic to a terrestrial lifestyle.

The box turtle, *Terrapene carolina* (L.), is found throughout the eastern United States. This small, terrestrial turtle has been studied more thoroughly than most reptile species, perhaps because of its ubiquity and innocuousness. The wealth of our knowledge on diet, habitat preference, and behavior makes the box turtle an excellent model for investigating parasite–host interactions (Stuart and Miller 1987).

This study was initiated to determine the following: (1) helminth intensity and prevalence in box turtles in North Carolina; (2) correlations, if any, of host age and sex with helminth intensity and prevalence; (3) similarity of helminth fauna in host specimens from North Carolina and elsewhere in the United States; and (4) helminth infection patterns in relation to box turtle behavior and dietary habits.

MATERIALS AND METHODS

Turtles were collected from 13 North Carolina counties between June 1982 and August 1989. Collecting was done primarily on the

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Piedmont Plateau ($n = 97$), with small comparative samples taken from the Blue Ridge Mountains ($n = 16$) and the Coastal Plain ($n = 4$). Ninety-seven turtles were collected either as roadkills or while they were crossing highways. Twenty specimens were collected in the field, in part with the aid of a border terrier dog trained to locate turtles by scent. All turtles were sexed by secondary sexual characteristics or grouped as juveniles if the plastron length was <100 mm. The turtles were weighed to the nearest 0.1 g, measured both along the straight length of the plastron and around the curve of the carapace, and examined for helminth parasites. The entire visceral mass was removed. The body cavity and each organ was examined separately. The gastrointestinal tract was separated into distinct sections (esophagus, stomach, intestines, and colon), and individual sections were cut lengthwise, washed, and examined separately. After removal of parasites from the lumen, each section was scraped with a sharp blade. The gut sections and the contents were digested in a pepsin-HCl solution agitated constantly for 1 hour at 36C. The solution was decanted, and the residue was examined for helminths with the aid of a stereoscopic microscope.

Stomach ulcerations were removed and fixed in 70% ethyl alcohol, 5% formalin, or glutaraldehyde before sectioning for histological analysis. Blood smears were strained with hemal blood film stain and examined for the presence of microfilariae.

Helminths were considered prominent if the prevalence was $>15\%$ and peripheral if the prevalence was $<15\%$. We used an ANOVA to test for significant differences in number of species of parasites between sexes. A Kruskal-Willis test was used to test for significant differences in number of individual parasites between sexes and geographical regions of the state.

RESULTS

The box turtles we examined consisted of 43 males, 48 females, and 26 juveniles. Stuart and Miller (1987) previously reported on mass, sex and age structure, seasonal distribution, reproduction, and food habits of 104 individuals from this collection. Of the 117 turtles, 3 were not infected, 27 were infected with 1 species of helminth parasite, 41 were infected with 2 species, and 46 were infected with >3 parasite species. The modal number of helminths was 22 with a range of 0–303, exclusive of larval *Spironoura affinis* in stomach ulcers. The helminth species we found and their prevalence and intensity are shown in Table 1. No significant differences were found in helminth species prevalence or intensity between host males, females, and juveniles. Four helminth species exhibited a prominent infection rate of $>15\%$:

Table 1. Helminths collected from 117 turtles from North Carolina.

Parasite	Infection				
	Number	Percent (%)	Range	\bar{x}	SE
Platyhelminthes: Digenea					
Brachycoeliidae					
<i>Brachycoelium salamandrae</i>	3/117	2.6	7-9	8.3	0.67
Telorchidae					
<i>Telorchis robustus</i>	35/117	30	1-295	37.5	10.8
Nematoda:					
Molineidae					
<i>Oswaldocruzia</i> sp.	97/117	83	1-38	7.3	0.73
Cosmocercoididae					
<i>Cosmocercoides dukae</i>	24/117	20.5	1-241	22.3	10.4
<i>Aplectana</i> sp.	7/117	6	1-15	4.0	1.8
Kathlaniidae					
<i>Spironoura affinis</i>	89/117	76	1-151	32.0	4.0
Camallanidae					
<i>Serpinema microcephalus</i>	1/117	0.9			
Physalopteridae					
<i>Physaloptera</i> sp.	3/117	2.6	1-3	2.67	.88
Acanthocephala					
Oligacanthorhynchidae					
<i>Macracanthorhynchus ingens</i>	1/117	0.9			

Oswaldocruzia sp. (82.9%), *Spironoura affinis* Leidy, 1856 (76.1%), *Telorchis robustus* Goldberger, 1991 (29.9%), and *Cosmocercoides dukae* (Holl, 1928) (20.5%). An additional five species were considered peripheral with a prevalence of <15%. No extraintestinal helminths or microfilariae were found.

We found a morphologically distinct and unnamed species of *Oswaldocruzia* in the stomach of box turtles. Spicular morphology differs substantially from *O. pipiens* Walton, 1929 from amphibian hosts. Both the spicules and the dorsal ray of males are substantially larger than those of *O. pipiens*, although the species in the box turtles is smaller in all other respects. The prevalence of infection was 82.9% (97/117), making this the most common helminth parasite encountered. The mean intensity of infection was 7.3 worms per infected turtle with no significant difference between any age or sex classes ($P = 0.30$).

Spironoura affinis infected 76.1% (89/117) with a mean intensity of 32 nematodes per turtle. The range in intensity was 1-151. The difference in intensity of infection with *S. affinis* was nearly significant between adults and juveniles ($P = .056$); means for males were 20 ± 4.0 (SE), females 17 ± 4.6 , and juveniles 34.7 ± 8.4 . Pairwise contrasts

using a Mann-Whitney U-test between males, females, and juveniles indicated that the number of *S. affinis* in juveniles differed significantly from that in females ($P = 0.02$) but that there was no significant difference between males and females ($P = 0.26$), or between juveniles and males ($P = 0.13$). Fifty-two (44%) of the 117 turtles had active ulcer-like lesions in the fundal region of the stomach. Macroscopically, the lesions or ulcers showed a raised area 1–2 cm in diameter with a central opening 4–5 mm wide that extended into the stomach wall. Microscopically, the lesions showed a moderate to dense lymphoid infiltrate into the granulomatous lining of the ulcer. When pressure was applied to the base of these ulcers, masses of larval nematodes were expressed. Comparison with adult and immature nematodes already collected from the colon, particularly in regard to the shape of the esophageal bulb and the developing lip structures, showed these larvae to be *Spironoura affinis*. Many of the turtles had healed from previous ulcers, which suggests that the damage is tolerated.

In our survey, 29.9% of the turtles (35/117) were parasitized by *Telorchis robustus*, including 13 males, 15 females, and 7 juveniles. The number of worms per turtle was substantial with a mean (and range) of 62.2 (1–295) for males, 22.5 (1–93) for females, and 27.5 (1–80) for juvenile turtles. *Telorchis robustus* caused the only serious health problem seen in our study. One turtle with 223 worms had a partially telescoped intestine, apparently caused by the large worm mass.

Two of the male turtles hosted nine and seven *Brachycoelium salamandrae* (Froelich, 1789), respectively. One female harbored nine worms. None was found in juvenile turtles. The total prevalence was 2.6% (3/117) with a mean of 8.3 worms per turtle.

Twenty-four of the box turtles were infected with *Cosmocercoides dukae* (range = 1–241, \bar{x} = 22.3). The genus *Aplectana* is closely related to *Cosmocercoides* and is usually distinguished from the latter by the absence of plectanes in the male. Both are normally parasites of amphibians. Five (4.3%) turtles were infected with 1–15 sexually mature nematodes, lacking plectanes on the males. Because of the absence of plectanes, these worms were tentatively identified as *Aplectana* sp., but additional work on the morphology and life cycle is needed before a firm identification of the species can be made.

We also found two genera of spirurid nematodes. *Serpinema* (= *Camallanus*) *microcephalus* (Dujardin, 1845) was in the stomach of one turtle. This host was partially buried in the mud in a pool in an intermittent stream. The turtle had possibly swallowed infected copepods. Three turtle stomachs contained *Physaloptera* sp. Only two males were recovered. Based on the small sample size, we could not determine

whether these specimens were the species described from *Terrapene ornata* by Hill (1941) as *P. terrapenis* Hill, 1941.

One turtle contained one immature specimen of the acanthocephalan *Macracanthorhynchus ingens* (Linstow, 1879). This worm was not attached to the stomach wall and was possibly a spurious parasite contracted by the turtle having recently eaten an infected beetle.

DISCUSSION

The life histories of most of the parasites collected in this study are poorly documented, and much of the literature is either contradictory or limited in scope. In addition, major disagreement exists concerning the appropriate nomenclature for many species or species complexes. To help clarify existing information and to place our results in perspective for future studies, a summary of nomenclatural problems and life history data follows.

PLATYHELMINTHES: DIGenea

Brachycoelium salamandrae (Froelich, 1789)—Both Harwood (1932) and Byrd (1937) described a number of species of *Brachycoelium* from reptiles and amphibians in the southeastern United States. Rankin (1938) reviewed the genus and concluded that the characters used to describe the various species were too variable to be of specific diagnostic value. Rankin (1945) also stated that the relative size of individual flukes was dependent on the number of flukes infecting a particular host. The worms were quite small when large numbers were present but were substantially larger when ≤ 20 were present. Rankin advocated that *Brachycoelium daviesi* Harwood, 1932; *B. dorsale* Byrd, 1937; *B. georgianum* Byrd, 1937; *B. hospitale* Stafford, 1900; *B. louisianae* Byrd, 1937; *B. meridionalis* Harwood, 1932; *B. mesorchium* Byrd, 1937; *B. obesum* Nicoll, 1914; *B. ovale* Byrd, 1937; *B. storeriae* Harwood, 1932; and *B. trituri* Holl, 1928 be reduced to synonyms of *B. salamandrae*. Cheng (1958) disagreed, recognized all of the above listed species, and described a new species, *Brachycoelium elongatum* Cheng, 1958. Since that time, two additional species have been described: *B. stablefordi* Cheng and Chase, 1961 and *B. ambystomae* Couch, 1966. All specimens found in the box turtles in our study were identified with Cheng's keys as *Brachycoelium salamandrae*. Here, we follow Rankin in treating this species complex as a single, extremely variable species whose morphological features are influenced by numbers and hosts.

Brachycoelium salamandrae has been reported from a wide range of reptile and amphibian species. Rumbold (1928) reported *B. salamandrae* as the only trematode he found in seven box turtles from North Carolina, with an infection rate of 28% and an average of 0.28 worms

per turtle. Raush (1947) examined 19 box turtles in Ohio and found one turtle to host 27 specimens of *B. salamandrae*. Rankin (1945) listed the species distribution as worldwide, but Yamaguti (1971) listed only Palearctic and Nearctic hosts. Rankin (1945) noted a correlation between the terrestrial habits of certain amphibian hosts and a high level of prevalence, suggesting that terrestrial invertebrates were probably involved in transmission. Denton (1962) reported snails and slugs, *Praticollela berlandieriana* (Moricand), *Derocerceras reticulatum* (= *Agriolimax agrestis*) (Mier), and *Mesodon thyroideus* (Say) as suitable experimental first intermediate hosts. Both motile and encysted cercariae were shed in secreted mucus. Uninfected *P. berlandieriana*, *D. reticulatum*, *Triodopsis texasiana* (= *Polygyra texasiana*) (Moricand), *Anguispira alternata* (Say), and *Bulimulus alternatus* (Say) became infected within 2–10 days after being exposed to infected first intermediate hosts, thus serving as second intermediate hosts. Jordan (1963) and Jordan and Byrd (1967) added *Triodopsis caroliensis* (Lea) and *Mesodon inflectus* (Say) to the list of first intermediate hosts and *T. caroliensis*, *M. inflectus*, *Zonitoides aboreus* (Say), *Gastrocopta contracta* (Say), *Stenotrema barbigerrum* (Redfield), *Philomycus carolianus* (Bosc), and *Deroceras laeve* (Müller) as second intermediate hosts. Cheng (1958) reported development of nonencysted metacercariae in *Ventridens ligera* (= *Zonitoides ligerus*) (Say). The definitive host presumably becomes infected by consuming snails with encysted metacercariae, because both Klimstra and Newsome (1960) and Stuart and Miller (1987) found that gastropods comprise a large percentage of box turtle diets. Given the broad range of first and second intermediate hosts that *B. salamandrae* is capable of infecting and the high frequency of these taxa in box turtle diets, it is surprising that the prevalence of infection is so low.

Telorchis robustus Goldberger, 1911—Wharton (1940) redefined the genus *Telorchis* and its species. We used his species key to identify *Telorchis robustus* from the box turtles in our study. Goldberger (1911) described *T. robustus* from a box turtle collected in Maryland, and Krull (1936) stated the trematode was common in Maryland box turtles. Bennett and Sharp (1938) found *T. robustus* in 38% (13/34) of *Terrapene c. triunguis* (Agassiz) examined in Louisiana. The number of worms ranged from three to nine, with an average of five worms per turtle. They also reported *T. robustus* from 12% (8/65) *Sternotherus odoratus* (Latreille) with an average infected of 10 worms per animal and a range of 1–28. Rausch (1947) reported *Telorchis* sp. from 1 of 19 box turtles in Ohio and *T. robustus* in four of eight *Clemmys guttata* (Schneider). The latter averaged two worms per turtle with a maximum of four. Thirteen of 35 turtles in our study had ≥ 25 worms

in the small intestines, which is substantially more than found in previous studies. The number of worms per turtle was substantial with a mean (and range) of 62.2 (1–295) for males, 22.5(1–93) for females, and 27.5 (1–80) for juvenile turtles. We do not know why the mean number of this trematode is so much higher in North Carolina box turtles than that reported from other localities or other species of turtles.

Krull (1935, 1936) reported that *Pseudosuccinea columella* (Say) became infected after eating trematode eggs (experimental infection) and began to shed xiphidiocercariae within 28–32 days. Cercariae successfully penetrated and encysted as metacercariae in three snail species: *P. columella*, *Helisoma trivolvis* (Say), and *Lymnaea traskii* (Lea). Krull postulated that turtles were infected during the spring and early summer when they ate snails in semi-flooded flats. He also noted that metacercariae were never abundant, although snails had been repeatedly exposed to thousands of cercariae. However, he did report that one snail would occasionally acquire a much heavier infection than others in the same group perhaps because they began feeding more quickly than others. In light of more recent studies on host immunity, genetic susceptibility might be a more reasonable cause than a behavioral trait. In either case, these “super-infected” snails will influence the range of worms in infected definitive hosts.

NEMATODA

Oswaldocruzia sp.—Seven species of *Oswaldocruzia* have been described from North American amphibians and reptiles (Baker 1977): *O. subauricularis* Travassos, 1917; *O. leidy* Travassos, 1917; *O. pipiens* Walton, 1929; *O. collaris* Walton, 1929; *O. waltoni* Ingles, 1936; *O. euryceae* Reiber, Byrd, and Parker, 1940; and *O. minuta* Walton, 1941. *Oswaldocruzia subauricularis* is a neotropical species and has only been reported once in the United States. Baker (1977) redescribed *O. pipiens* and regarded *O. collaris* and *O. eurycea* as synonyms of *O. pipiens*. He also treated *O. waltoni* and *O. minuta* as species inquirendae and *O. leidy* as a nomen nudum. Accounts of developmental and transmission patterns in *Oswaldocruzia* vary widely. Baer (1952) stated that *O. fillicollis* (Goeze) (presumably referring to *Oswaldocruzia filiformis* [Goeze, 1782] from amphibians molted twice within the egg and was thus infective when the egg was consumed. Baer also noted that L_3 larvae might sometimes hatch and remain ensheathed in the preceding molt until consumed. Baker (1978a) reported that eggs from frogs and toads were laid in the 16–cell stage, and L_1 larvae hatched within 24 hours of passage in the host's feces. Laboratory cultured specimens developed to the ensheathed, infective L_3 stage within 3–4 days at room temperature. Anuran infection occurs via

skin penetration. Larvae attached initially to the stomach mucosa but migrated posteriorly to the intestine as they matured. Baker felt that late summer and early fall, when marsh size was reduced and frog density was highest, was the most important period for parasite transmission and that *O. pipiens* could overwinter in its host. Hendrixx (1981) studied the seasonal fluctuation of *O. filliformis* in *Bufo bufo* L. in the Netherlands, and he reported L₄ larvae embedded in the stomach mucosa of overwintering hosts.

Oswaldocruzia specimens were only rarely found outside the stomach in the box turtles of our study. An infective mode involving skin penetration, while feasible in an amphibian, is somewhat more difficult to accept in the heavily armored box turtle. While softer areas of skin are found around the base of the legs and throat, chance nematode access and penetration could scarcely account for the very high levels of infection. The habits and habitats of the extremely wide range of amphibian and reptile hosts of *Oswaldocruzia* provide additional reasons to suspect an alternate route of infection. *Storeria dekayi* (Holbrook), *S. occipitamaculata* (Storer), *Anolis carolinensis* (Voigt), many ranid and bufonid species, *Typhlotriton spelaeus* Stejneger, and *Terrapene carolina* use a broad spectrum of habitats including semi-fossorial, arboreal, aquatic, semi-aquatic, cave-dwelling, and terrestrial. These habitat differences alone would severely hamper transmission of a parasite dependent on skin penetration to infect. Circumstantial evidence based on host diversity and host diet suggests that *Oswaldocruzia* might use an alternate life cycle with gastropods as intermediate hosts. In support of this contention, we found a small male *Oswaldocruzia* completely embedded in a piece of snail tissue taken from the stomach of a freshly killed box turtle. While as yet unproven, morphological and biological differences in the parasites and the different hosts suggest that the species of *Oswaldocruzia* in box turtles is distinct from *O. pipiens*.

Spironoura affinis Leidy, 1856—Leidy (1856) erected the genus *Spironoura* and listed two species: *S. gracile* from the stomach of the red-bellied turtle, *Pseudemys rubriventris* (Le Conte) (= *Emys serata*) and *S. affine*, later modified to *S. affinis* by Yamaguti (1961), from the cecum of the box turtle, *Terrapene carolina* (= *Cistudo carolina*). Yorke and Maplestone (1926) designated *S. gracile* as the type species apparently because it appeared first in Leidy's manuscript. This species has not, however, been collected since its description. Freitas and Lent (1942) felt that *S. gracile* should be considered a species inquirendum since Leidy's description was brief and incomplete. They proposed revalidation of the genus *Falcaustra* Lane, 1915 with all of the species of *Spironoura* transferred to this genus. Some authorities (Yamaguti

1961, Skrjabin et al. 1964) rejected this, but Chabaud (1978) considered *Falcaustra* to be the valid genus for this group. We follow Chapin (1924) in rejecting *Falcaustra* and continue to use *Spironoura* because Leidy's original description, although brief by today's standards, is sufficient to distinguish the genus, giving *Spironoura* priority.

About 50 species of *Spironoura* have been described from fishes, reptiles, and amphibians worldwide (Skrjabin et al. 1964). Mackin (1936) published a thorough study of the anatomy of the genus *Spironoura* and a key to the species from the United States. Five species of *Spironoura* have been reported from *Terrapene carolina* in the United States: *Spironoura affinis* Leidy, 1856; *S. longispicula* (Walton, 1927); *S. cryptobranchi* Walton, 1930; *S. chelydrae* (Harwood, 1930); and *S. concinnae* Mackin, 1936. Canavan (1929) described *S. procera* from the same host, *Pseudemys rubriventris* (= *Emys serata*), and from the same locality where Leidy worked, i.e., Philadelphia. Harwood (1930) is the only other investigator to have reported the presence of *Spironoura procera*, but he said that it was not sufficiently distinct from *S. affinis* to merit specific status. Harwood's (1932) work, plus our own study of *S. affinis* and examination of the specimen from the U.S. National Museum Helminthological Collection, Beltsville, Maryland marked "*Spironoura procera*? (No. 52145)," suggest that *S. affinis*, *S. procera*, and *S. gracile* are all members of the same species. We also borrowed specimens identified as *S. concinnae*, collected from *Terrapene carolina* in Mississippi, from the U.S. National Museum Helminthological Collection (No. 66152). Comparison with specimens of *S. affinis* collected from the same host in North Carolina convinced us that Caballero (1939) was correct in considering *S. concinnae* as a synonym of *S. affinis*. We have followed Yamaguti's (1961) designation of *Spironoura affinis* to minimize confusion. However, this diverse and complex genus needs revision.

Cosmocercoides dukae (Holl, 1928)—*Cosmocercoides dukae* is a common parasite of amphibians. Holl (1928) originally described *C. dukae* (= *Cosmocerca dukae*) from a newt collected in Durham, North Carolina. Harwood (1932), apparently unaware of Holl's work, described the same species as *Oxysomatium variabilis* and listed 10 species of amphibian and reptile hosts. Harwood's experimental attempts to demonstrate host infection by skin penetration were not successful, but he felt that a direct life cycle was probable. Ogren (1953, 1959) demonstrated the nematode's ability to complete its life cycle in a variety of gastropod species, including *Ashmunella rhyssa* (Dall), *Triodopsis* (= *Polygyra*) *fosteri* (Baker), *Retinella* sp. Fischer, and *Deroceras* sp. Rafinesque. Anderson (1960) described the life cycle of *C. dukae* in *Discus cronkhitei* (Newcombe), *Zonitoides aboreus* (Say), and *Deroceras*

Table 2. Helminths reported from *Terrapene carolina*.

Parasite	Number Infected/Examined	Locality	Reference
MONOGENEA			
Polystomidae			
<i>Neopolystoma terrapenis</i> (Harwood, 1932)	1/14	Tex.	Harwood (1932)
<i>Polystomoidella oblongum</i> (Wright, 1879)	1/16	La.	Acholonu (1969)
<i>P. whartoni</i> (Price, 1939)	1/16	La.	Acholonu (1969)
<i>Polystomoides coronatum</i> (Leidy, 1888)			Braun (1890) (from Ernst and Ernst 1977)
DIGENEA			
Brachycoeliidae			
<i>Brachycoelium salamandrae</i> (Froelich, 1789)	2/7	N.C.	Rumbold (1928)
	1/19	Oh.	Rausch (1947)
Telorchidae			
<i>Telorchis</i> sp.	1/19	Oh.	Rausch (1947)
<i>T. corti</i> Stunkard, 1915	2/63	Ill.	Martin (1973)
<i>T. robustus</i> Goldberger, 1911	common	Md.	Goldberger (1911); Krull (1935, 1936)
	13/34	La.	Bennett and Sharp (1938)
CESTOIDEA			
Protocephalidae			
<i>Proteocephalus</i> sp.	1/14	Tex.	Harwood (1932)
Anoplocephalidae			
<i>Oochoristica whitentoni</i> Steelman, 1939	1/12	Ok.	Steelman (1939)
immature cyclophyllidean	1/34	La.	Bennett and Sharp (1938)
NEMATODA			
Dipetalonematidae			
<i>Cardianema cistudinis</i> (Leidy, 1856)		Penn.?	Leidy (1856)
		D.C.	Alicata (1933)
	1/4	La.	Herban and Yeager (1969)
Atractidae			
<i>Atractis carolinae</i> Harwood, 1932	13/14	Tex.	Harwood (1932)

Table 2. Continued.

	Number Infected/Examined	Locality	Reference
Cosmocercidae			
<i>Aplectana</i> sp.	7/7	N.C.	Rumbold (1928)
	1/19	Oh.	Rausch (1947)
	12/16	La.	Acholonu and Amy (1970)
<i>Cosmocercoides dukae</i> (Holl, 1928)	7/14	Tex.	Harwood (1930, 1932)
	1/19	Oh.	Rausch (1947)
Kathlaniidae			
<i>Cruzia testudines</i> Harwood, 1932	13/14	Tex.	Harwood (1932)
<i>Spironoura</i> sp. Leidy, 1856	11/63	Ill.	Martin (1973)
		Md.	Ernst and Ernst (1975)
<i>S. affinis</i> Leidy, 1856		Penn.	Leidy (1856) Boulenger (1923)
	13/14	Tex.	Harwood (1932)
	9/19	Oh.	Rausch (1947)
	6/63	Ill.	Martin (1973)
<i>S. chelydrae</i> Harwood, 1932	4/5	Tenn.	Limsuwan and Dunn (1978)
<i>S. cryptobranchi</i> Walton, 1930		La.	Bennett and Sharp (1938)
<i>S. longispiculata</i> Walton, 1927		Penn.?	Walton (1927)
Molineidae			
<i>Oswaldocruzia leidy</i> Travassos, 1917		Penn.?	Leidy (1856)
		La.?	Steiner (1924)
	2/7	N.C.	Rumbold (1928)
	10/19	Oh.	Rausch (1947)
	3/16	La.	Acholonu and Amy (1970)
		Md.	Ernst and Ernst (1975)
<i>O. pipiens</i> Walton, 1929	2/14	Tex.	Harwood (1932)
<i>O. leidy</i> & <i>O. pipiens</i>	10/63	Ill.	Martin (1973)
Camallanidae			
<i>Serpinema microcephalus</i> (Dujardin, 1845)	2/16	La.	Acholonu and Amy (1970)
	7/63	Ill.	Martin (1973)

Table 2. Continued.

	Number Infected/Examined	Locality	Reference
Physalopteridae			
<i>Physaloptera terrapenis</i> Hill, 1941	7/47 in	Ok.	Hill (1941)
<i>T. ornata</i>			
Spiruridae			
<i>Spiroxys constricta</i> (Leidy, 1856)	7/16	La.	Acholonu and Amy (1970)
		Penn.?	Leidy (1856)
<i>S. contorta</i> (Rudolphi, 1819)	11/63	Ill.	Martin (1973)
Gnathostomatidae			
<i>Gnathostoma procyonis</i> Chandler, 1942	3/4	La.	Ash (1962)

laeve (Müller) (= *D. gracile* Rafinesque) and suggested that amphibian infections occurred from ingestion of infected molluscs. Baker (1978b) reported that *C. dukae* larvae burrow through the skin of toads and migrate through the body. This versatility in ability to use such different definitive hosts suggested to Baker that *C. dukae* represented an early stage of parasitic adaptation.

PARASITES AND HOST DIET

Surveys from various areas within the range of *Terrapene carolina* indicate that a broad range of helminth parasites infect the box turtle (Table 2). In North Carolina, parasite presence appears to be regulated primarily by diet. Recognizable items found in the gastrointestinal tract of 72 turtles, in order of frequency of occurrence, were snails (Gastropoda) - 59%, insects (Insecta) - 43%, sowbugs (Isopoda) - 40%, plant material (primarily fungi) - 32%, slugs (Gastropoda) - 7%, rodents (Mammalia) - 5.5%, earthworms (Oligochaeta) - 3%, and millipeds (Diplopoda) - 3%. *Cosmocercoides dukae*, *Brachycoelium* spp., and *Telorchis robustus* have all been shown to use molluscan intermediate hosts (Krull 1935, 1936; Ogren 1953; Jordan and Byrd 1967). Our evidence strongly suggests that *Spironora affinis* and *Oswaldocruzia* sp. also might be capable of using molluscs to reach the definitive host. The records for *Serpinema microcephallus* and *Physaloptera* sp. probably represent rare or accidental infections. The life cycle of most physalopterans is unknown; those that are known use invertebrate intermediate hosts. The specimen of *Macroacanthorhynchus ingens* indicates recent ingestion of a scarabid beetle. Considering the relatively high incidence of insects and sowbugs in the diet and the semi-aquatic nature of the turtles, the absence of acanthocephalans is some-

what surprising. The poisonous fungi in the diet could conceivably act as a periodic vermifuge, but that has not been investigated.

Parasite life cycles are often complex and may involve a variety of strategies to get the parasite into the definitive host, including one or more intermediate hosts. Successful transmission requires a congruence between parasite life cycle and host behavior or ecology. Aho (1990) discussed the importance of reptile- and amphibian-parasite systems in understanding the ecological and evolutionary relationships which determine parasite species distribution. The parasite presence/absence data accumulated in our study suggest that *Spironoura affinis* has a long history or relationship with *Terrapene carolina* and the aquatic emydid turtles from which the box turtle evolved. Nursery ulcers and molluscan intermediate hosts could represent the nematode's adaptation to the host's move from an aquatic to a terrestrial habitat. The presence/absence data also suggest that *Terrapene carolina* acquired a number of amphibian parasites in the ecological shift from water to land.

ACKNOWLEDGMENTS—This study was supported in part by Science and Engineering Development Award 89SE01 from the North Carolina Board of Science and Technology. We are indebted to J. Ralph Lichtenfels for the loan of specimens from the U.S. National Museum Helminthological Collection. We further thank James W. Petranks for assistance with statistical analyses, John G. Petranks for updating the molluscan nomenclature, and to Joyce McHenry, Jeanne Simmons, and Kathy Haley for assistance in collecting specimens.

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Accepted 4 May 1992

Notes on the Spiny Softshell, *Apalone spinifera*
(Testudines: Trionychidae), in Southeastern Virginia

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ABSTRACT—The Gulf Coast spiny softshell turtle (*Apalone spinifera aspera*), collected in Lake Whitehurst, Norfolk, Virginia, represents the first record of this subspecies for the state. The eastern spiny softshell (*Apalone spinifera spinifera*) occurs naturally in the Tennessee and Ohio drainages in southwestern Virginia. Based on available evidence, the Norfolk population and a population of the nominate subspecies in Isle of Wight County, Virginia, also reported here, should be considered isolated, introduced, and established populations.

Apalone spinifera is a wide-ranging species in North America occurring from the Rio Grande River northeastward through the midwest to the Great Lakes region and eastward through the Carolinas to the Atlantic Ocean (Ernst and Barbour 1972, Conant and Collins 1991). Seven subspecies are recognized (Ernst and Barbour 1989, Iverson 1992), of which one, *Apalone spinifera spinifera*, occurs naturally in the Tennessee River drainage in southwestern Virginia (Tobey 1985). Recent discoveries of populations of this species in southeastern Virginia raise questions about the occurrence of a second subspecies in the state and demonstrate that introduced populations can become established in this area.

On 25 June 1991, a large female *A. spinifera spinifera* (370 mm carapace length [CL], 283 mm plastron length [PL], and 5.5 kg body mass) was discovered adjacent to a commercial fish rearing pond, 4.8 km east of Windsor, Isle of Wight County, Virginia; she was released. Subsequent observations (5 July and 24 October 1991) and captures (9 November 1991) revealed at least four other adults (a male 262 mm CL, 184 mm PL, 1,550 g, The Living Museum, Newport News, Virginia) and one juvenile (111 mm CL, 85 mm PL, National

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Museum of Natural History, USNM 314209) in several rearing ponds on the same site. The hatchery owner could not verify time or source (e.g., shipments of commercial fish) of the turtles. He noted that they have been present for several years.

The discovery of another population in southeastern Virginia is comparatively more perplexing. In October 1988, an unidentified soft-shell turtle was observed in Lake Whitehurst, City of Norfolk, Virginia (T. Pitchford, personal communication, Virginia Beach Marine Science Museum). Softshells were confirmed in this lake on 2 August 1991 when an adult male *A. spinifera aspera* (196 mm CL, 134 mm PL, 574 g body mass, USNM 314210) was collected on hook and line. A large female was taken by another fisherman between 13 August and 1 September 1991 but it escaped, and its identity cannot be confirmed. Three juveniles found beneath a boat dock on Lake Whitehurst near Shore Drive on 21 September 1991 were given to the junior author by a local boy who said that the turtles were coming out of the sand. The juveniles averaged 51.0 ± 2.0 (SD) mm CL (range = 49–53), 35 ± 1.0 mm PL (range = 34–36), and 13 g ($n = 1$) body mass. A recent hatchling (38.9 mm CL, 26.6 mm PL, 6 g) was caught in the same area on 12 October 1991. Softshells apparently do not overwinter in the nest in this area, although they may in the upper midwest (Gibbons and Nelson 1978).

The nearest population of *A. spinifer aspera* is in Harnett County, North Carolina, 290 km southwest of Norfolk (A. S. Braswell, personal communication, North Carolina Museum of Natural Sciences). Our Lake Whitehurst records establish *A. s. aspera* for the first time in Virginia and indicate a substantial distributional hiatus between south-central North Carolina and southeastern Virginia.

Is the Norfolk population introduced or is it a heretofore undocumented natural population? Intensive sampling with large nets during 1977–91 by the Virginia Department of Game and Inland Fisheries revealed no softshells. However, most sampling occurred in early spring (March to early April) before most freshwater turtles and presumably softshells (see Robinson and Murphy 1978) become active in this area (J. C. Mitchell, unpublished data). This particular sampling effort yielded few turtles of any species (R. Southwick, personal observation). Considerable effort has been expended in North Carolina and Virginia to determine the distributions of reptilian species within these states (W. M. Palmer and A. L. Braswell, personal communications; J. C. Mitchell and C. A. Pague, unpublished data). In addition, the area of southeastern Virginia and northeastern North Carolina has been a favorite collecting area for decades (e.g., Nemuras 1964; W. M. Palmer and R. de Rageot, personal communication). If present earlier, softshells should have been

found. Thus, the likelihood of intentional release of pet trade softshells into Lake Whitehurst cannot be discounted. A presumably introduced specimen of *A. s. spinifera* (George Mason University Collection, GMU 1676) was found in Bull Run Creek, Fairfax County, Virginia in July 1982.

A population of *Apalone spinifera* became established after 1910 in the Maurice River system in southern New Jersey (Conant 1961) and apparently continues to persist (Conant and Collins 1991). Populations in the Colorado River and several aquatic systems in California are also considered introduced (Linsdale and Gressitt 1937, Webb 1962, Stebbins 1985). These introductions indicate that the spiny softshell can survive in areas outside of its natural range and establish viable populations. Thus, until additional populations of *A. s. aspera* are discovered in southeastern Virginia and northeastern North Carolina, the Lake Whitehurst population should be considered an introduced population.

ACKNOWLEDGMENTS—We thank Joe St. Martin and Andrew Castellano for bringing the Lake Whitehurst softshells to our attention, Tom Pitchford for his initial observation of a softshell in Lake Whitehurst, and Sam Perry, of Perry's Minnow Farm, for allowing us access to his property to study turtles. Alvin Braswell of the North Carolina State Museum of Natural Sciences kindly provided locations of softshell populations in North Carolina. Carl H. Ernst allowed access to the George Mason University vertebrate collection.

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Accepted 15 May 1992

Range Expansion of the Tree Swallow,
Tachycineta bicolor (Passeriformes: Hirundinidae),
in the Southeastern United States

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ABSTRACT—Since the late 1800s and early part of this century when the tree swallow, *Tachycineta bicolor*, was a peripheral and sporadic breeding species in the southeastern United States, its range has expanded considerably. The precise reasons for the range expansion of this and other swallows in the Southeast is unclear. Land clearing, impoundments and other land use patterns, the re-introduction of beavers (*Castor canadensis*), and the use of bluebird (*Sialia sialis*) boxes by swallows as nest sites appear to have facilitated the expansion. Several different corridors of dispersal are noted; North Carolina represents the current frontier of range expansion in the Southeast.

The 1957 edition of the American Ornithologists' Union Checklist (AOU 1957) stated that the breeding range of the tree swallow (now *Tachycineta bicolor*) extended south to northwestern Tennessee, northern West Virginia, Virginia, central Maryland, and northeastern Pennsylvania. At the turn of the century the species rarely nested as far south as southwestern Kentucky (Fig. 1). The breeding range has expanded considerably since the 1950s, but this change in distribution is not well documented. By the early 1980s the southern limits of distribution were defined as northeastern Louisiana, westcentral Mississippi, Tennessee, and North Carolina, but the tree swallow was "generally sporadic or irregular as a breeder east of the Rocky Mountain states and south of the upper Mississippi and Ohio Valleys, or along the Atlantic coast south of Massachusetts" (AOU 1983).

At least in parts of the Southeast, tree swallows are currently undergoing a rapid range expansion and indications are that they will become common and widespread throughout much of the area during the coming decades. This pattern of range expansion has already been exhibited by several other species of swallows in the Southeast. The majority of the information presented here is from North Carolina, which is the current frontier of range expansion in the Southeast.

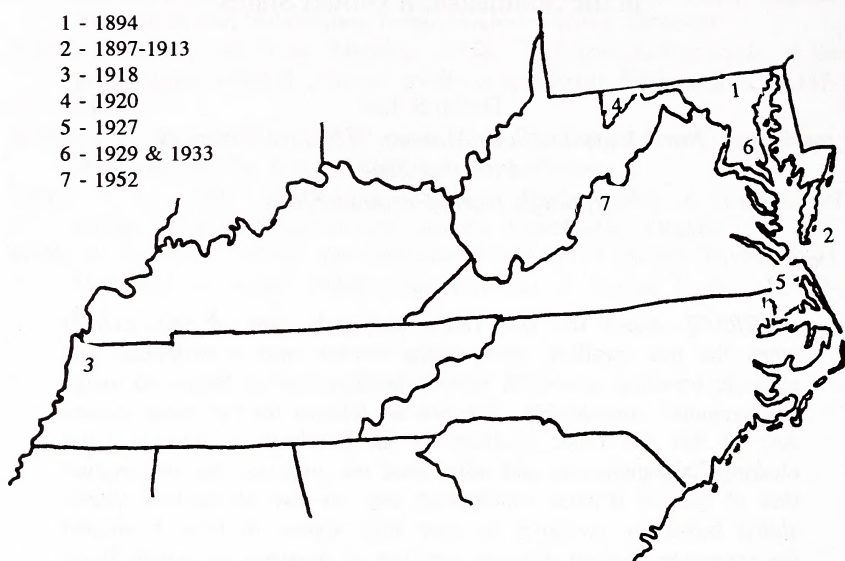


Fig. 1. Early isolated breeding records of tree swallows (*Tachycineta bicolor*) in the southeastern United States. See text for documentation sources.

METHODS

Information presented here is compiled from numerous published sources such as state bird journals and from unpublished records obtained from individuals and agencies monitoring bird distributions in the southeastern United States.

RESULTS

West Virginia—Hall (1983) notes that most West Virginia summer records are from the mountains where nests have been found near beaver ponds and other flooded sites. Definite nest records were given for Hampshire, Preston, Tucker, Randolph, and Pocahontas counties. Hall (1983) also reported nesting records outside the mountains from the McClintic Wildlife Station, Mason County (several occasions), at Belle, Kanawha County (1961), and Randolph County (1975). Additionally, there are summer sightings for Jefferson, Morgan, Pendleton, Greenbrier, Mercer, Wood, and Gilmer counties in West Virginia. These records indicate a considerable expansion since the 1957 AOU Checklist.

Maryland—Stewart and Robbins (1958) reported tree swallows as breeding commonly in the tidewater region of the southern Delmarva and as being uncommon or rare breeders in other tide-

water areas of Maryland's Coastal Plain. This species was first reported as breeding in this area in 1929 and 1933 (unpublished egg catalogue of E. J. Court; Court 1936), but based on Virginia records (see below) it was probably present some time before Court's report. A disjunct portion of the breeding range was also noted in the Allegheny Mountains (Garrett County) with five specific nesting localities listed (Stewart and Robbins 1958). Despite a moderate amount of fieldwork in western Maryland early in this century, the first report of mountain nesting was not until 1920 (Eifrig 1920) with subsequent records in 1936 (Brooks 1936). The earliest documented nesting in Maryland was 1894 (W. H. Fisher; in Stewart and Robbins 1958). Although it is not known when tree swallows first started nesting in Maryland, it was likely just before the turn of the century. The 1894 record is for Baltimore County and is probably from Dulaney Valley north of Towson, where Fisher did most of his fieldwork (Lee 1988). Interestingly, this area was not considered part of the tree swallow's range in 1958. In 1968 the distribution was essentially unchanged (Robbins and Van Velzen 1968). Since then, however, the species has expanded throughout the state. It is still most numerous in the mountains and in tidewater areas. Tree swallows are now locally common nesters in the Maryland Piedmont (Maryland Breeding Bird Atlas data). State-wide they were found in 393 of the 1,256 Atlas blocks (31.2%), and they were found in every county in the state (C. S. Robbins, personal communication). Colonization of most areas in Maryland seems to be dependent on the species ability to nest in bluebird boxes.

Kentucky—Despite the state's location in relation to the historic range of tree swallows (southern Illinois 1889, Missouri 1894, and Tennessee 1918), the species was essentially unknown as a breeding bird in Kentucky even by the mid-1960s (Mengel 1965). The only record for the state before the 1960s is from 1889 to 1925 when Pindar noted that tree swallows were present in Fulton County in the summer. This county is in the extreme western tip of the state along the Mississippi River and just north of Reelfoot Lake, the site of the first record for Tennessee (Pindar 1889, 1925). Mengel (1965) visited this area between 1941 and 1951 and, although he noted favorable habitat, he did not locate nesting birds. Breeding was again noted in 1905 in the Cumberland River Valley (Lyon County at Long Run Park in Jefferson County) in 1975 (Monroe et al. 1988). The species is now recorded as nesting in scattered localities throughout the state. Its nesting is mostly along edges of lakes and rivers where there are many dead trees, and recently the species has been found using nest boxes (Monroe et al. 1988).

Virginia—In the early part of this century, Bailey (1913) recorded the tree swallow as nesting only on the lower Delmarva portion of Virginia where it bred mostly on islands. Murray (1952) summarized the historical nesting status in Virginia as follows: "There is one nesting record for Princess Ann County, June 15, 1927, upper end of Back Bay, Lewis; and one for Aylett, King William County, no date (Auk 14, 408). Palmer found a nest with young on Smith Island, June 10, 1897; and reports one with eggs, May 1894 (Auk 14, 408). Brooks states that it is a 'fairly common summer resident at the higher elevations at least in Highland County (Raven 6, 11–12, 2).'"

By the late 1970s Larner et al. (1979) noted that the tree swallow was locally common in the Virginia portion of the Delmarva Peninsula and rare elsewhere in the Coastal Plain. In the Piedmont it was a rare and local summer resident, and the first breeding record "in recent years" was recorded in Madison County in 1976. Larner et al. (1979) reported records in the mountains from Augusta, Highland, Russell, and Tazewell counties. In the last decade this species has greatly expanded its range in Virginia with confirmed nesting records in 34 counties (65+ sites) throughout the state and expected or presumed nesting in at least 18 additional counties (Sue Ridd, personal communication 1988; Virginia Breeding Bird Atlas).

Tennessee—The first nest was discovered at Reelfoot Lake, Tennessee, on 22 May 1918 (Ganier 1964) but from that time until 1968 no additional nests were reported; there was only one other observation of these swallows during the breeding season. Olson (1968) found an active nest at Norris Lake in Anderson County in 1968, and the same year Gray (1968) found a nest at Monsanto Ponds in Maury County. The early records were from the western part of the state adjacent to the Mississippi River. Since 1968 nests have been reported in Tennessee almost annually. Nicholson and Pitts (1982) summarized the distribution of nesting in Tennessee, noting that in recent years tree swallows have nested throughout the state.

North Carolina—In North Carolina tree swallows were first reported nesting in 1979 in the extreme northwestern corner of the state (LeGrand and Potter 1980). The nest was in an abandoned woodpecker cavity along the New River in Ashe County (elevation 9,100 m). The second record was nearly 192 km southeast of this site, and 2.4 km north of Asheville in Buncombe County near the French Broad River (elevation 600 m) in 1981 (Duyck 1981). In the subsequent decade the breeding range has expanded considerably.

Breeding Bird Atlas volunteers in North Carolina found tree swallows nesting in the mountains in the southwestern part of the state in Transylvania County (four locations) and in Henderson County.

Nesting was recorded in 1988 and 1989 and will probably continue in the future. In 1988 and 1989 a pair nested in a purple martin (*Progne subis*) gourd in Cowee Valley, Macon County, and in 1990 a pair nested in a bluebird box near Piney Creek, Alleghany County (Chat 55:64–65). The Piedmont birds were seen nesting in woodpecker cavities in trees killed during flooding to create Jordan Lake in Chatham County in 1988. A nesting pair was found in Vance County in 1990. To date these are the only confirmed nesting birds in the Piedmont. In the Coastal Plain, tree swallows were found nesting in eight locations in Currituck County (1989–90), and were seen during the nesting season in Pamlico County (1988) and along the lower Cape Fear River in Brunswick County (1990). In the Coastal Plain pairs of tree swallows used bluebird boxes and natural cavities in trees killed by impoundment and where natural flooding occurred along rivers and in salt marshes.

DISCUSSION

Although present day land-use patterns provide fields and other open areas suitable for swallow foraging, this alone does not account for the current, explosive range expansion because land clearing was widespread in the Southeast by the early 1800s. Nest sites are critical, and the same land-clearing patterns that provide open areas can also eliminate snags and other potential cavity-nest sites. The elimination of beavers from most of the Southeast at the turn of the century eliminated the potential for natural snags in areas impounded by beavers. Dead trees resulting from flooding in tidewater areas and adjacent salt marshes seem to have provided a natural dispersal route in coastal areas. Therefore it is interesting, and not easy to explain, that, despite the availability of natural habitat, tree swallows have only recently (since 1913 in Virginia; late 1980s in North Carolina) expanded in tidewater areas. It is to be expected that coastal tree swallows will also follow river systems inland and make use of dead trees in impoundments and beaver ponds in the Coastal Plain.

Phenology—Tree swallows are relatively early to late spring and early to late fall migrants, making it difficult to distinguish resident breeding birds from migrants. In Currituck County, North Carolina, in June 1990 I observed resident birds using cavities before, during, and after a fairly extensive northern migration of large numbers of transients. Nicholson and Pitts (1982) noted tree swallows at Reelfoot Lake, Tennessee, by mid-March, and territorial birds by late April when northbound migrants were still present. Southward migration in the southeastern United States begins in early July (Nicholson and Pitts

1982, personal observations). Major fall migration occurs in October, and birds winter in much of the Southeast, particularly along coastal areas.

Nesting dates in the Southeast range from 12 May to 3 July with no indication that pairs at southern latitudes nest any earlier than those to the north. The earliest recorded egg date, for example, is from Maryland (see below). Birds reported in from North Carolina (NCSM records) nested from early May through mid-June. The following is a list of nesting dates for the Southeast: 4 May–21 June, nesting activity (15–20 May eggs laid), North Carolina (Duyck 1981); 6 June, adult feeds fledglings, Tennessee (Williams 1976); 9 June, adult feeding young, Tennessee (Nicholson and Pitts 1982); 16 June, adult and fledged young, Tennessee (Nicholson and Pitts 1982); 9 June, adult at nest, North Carolina (Chat 44:9); 11 June, young birds being fed, North Carolina (Chat 44:9); early July, feeding young, Tennessee (Nicholson and Pitts 1982); early May to mid-July (egg dates 24 April–5 July, nestling 20 May–27 July), Maryland (based on 320 Maryland nest records, C. S. Robbins, personal communication).

Pattern of Range Expansion—Apparently the expansion of nesting into the outer Coastal Plain of Maryland, Virginia, and North Carolina, the southern Appalachians, Maryland, to North Carolina, and the Piedmont regions of these states occurred independently (Fig. 2). Sites along major rivers and those adjacent to cleared agricultural areas were the first to be colonized (i.e., 1889–1918 Mississippi River lowlands). Colonization occurred rather rapidly in the mountains (1920–36 Maryland, by 1929 in Virginia, and northern West Virginia pre-1957), and accelerated in the last decade (northern North Carolina in 1979 to southwestern North Carolina by 1988). Many of these sites were along rivers in the Mississippi basin.

In the Coastal Plain the species was nesting on the Delmarva as early as 1897, but was not common or widespread even by the 1950s and did not become so until the 1970s. Breeding individuals did not invade northeastern North Carolina until the late 1980s.

Their occurrence in the Piedmont seems sporadic. The earliest Piedmont record from the Southeast and Atlantic states is 1894 (Maryland), but the birds did not become established. Piedmont nesting was not documented until 1961 (West Virginia) and 1976 (Virginia) and was not widespread until the 1980s (Maryland and Virginia). This swallow is still uncommon the North Carolina Piedmont where it is known from only two sites. West of the Appalachians, this species had a similar history in Tennessee where the first nest was reported in 1918 with no new records until the second half of the 20th Century. Yet the species was nesting throughout Tennessee by 1982.

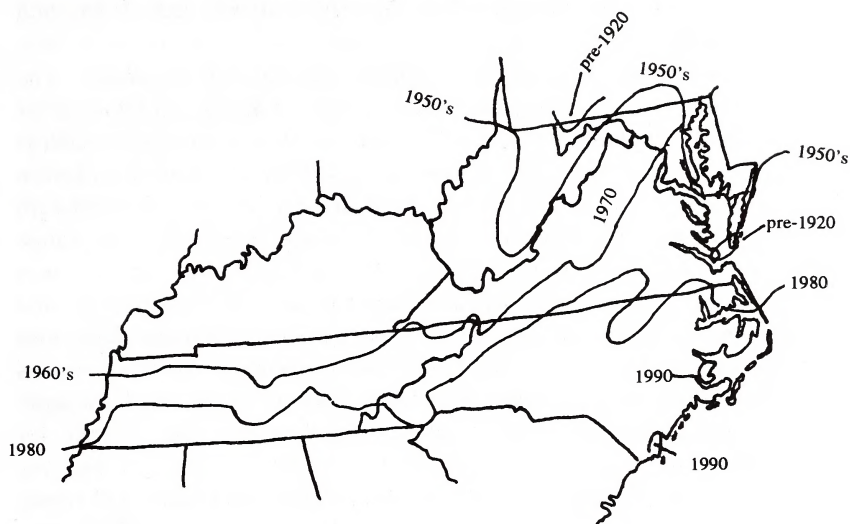


Fig. 2. The expanding breeding distribution of the tree swallow (*Tachycineta bicolor*) in the southeastern United States (1894-1991).

Possible Explanation for Range Expansion—Tree swallows might now be imprinted on bluebird boxes as nesting sites, and this imprinting possibly has allowed them to expand their range into areas where the lack of natural cavities would otherwise inhibit nesting.

Plasticity in food habits may also be important in the range expansion of this swallow. Lee and Franz (1972) reported on a pre-migration staging flock of several thousand tree swallows feeding over a cornfield on the eastern shore of Maryland. Examination of the stomachs of a dozen birds revealed corn flea beetles (*Chaetocnema pulicaria*). No other food items were found. Food items were counted in one stomach, and 170 corn flea beetles were found. Although I am not aware of other direct observations of tree swallows benefiting from agriculture or agricultural pests, at the minimum the clearing of land for agricultural purposes has created foraging areas not available in the precolonial period.

Several nesting sites are associated with man-made lakes and large impoundments constructed for waterfowl. Many hardwood trees killed by floodwaters contain cavities made by woodpeckers that provide multiple nest sites where the swallows form small colonies of a dozen or more pairs. Although the beaver was reintroduced by various state wildlife agencies and has made an explosive come-back, this generally precedes the period of range expansion of tree swallows outlined

here (see Bonwil and Owens 1939, Mansueti 1950, Lee 1988, and Lee et al. 1982).

Similar Range Expansion of Other Species of Swallows—The relatively rapid range expansion parallels the changing distribution of other swallows in the Southeast. The barn swallow's (*Hirundo rustica*) breeding range was largely to the north of North Carolina before 1942 (Pearson et al. 1942), but it bred locally in the mountains in the northwestern corner of the state and along the coast. The range expansion in the state was undocumented. By 1975 the species was colonizing the outer Coastal Plain in southeastern North Carolina, and today it occurs statewide (personal observation). Although they nest in barns and under docks, the main factor allowing dispersal seems to be the replacement of wooden bridges with concrete ones throughout the state (1960s-70s); the swallows use the concrete bridges for nest substrate.

At the beginning of this century cliff swallows (*Hirundo pyrrhonota*) were only transients in North Carolina. In 1967 they were reported nesting in the state, and by 1983 they had expanded their range in the Piedmont to Greensboro, Guilford County (Hendrickson 1984). They had previously been reported nesting at other Piedmont sites, all around reservoirs (Lake Cammack, Hycos Reservoir, McGehee's Mill, and Jordan Lake). They also nest at Falls Lake, Wake County (NCSM records, 1989). Like tree swallows, this species did not simply expand its range from north to south or from the west to the east as one might expect. They colonized scattered sites in the Piedmont and later colonized suitable adjacent sites. McConnell (1981) first reported nesting in the Mountains of North Carolina and noted a preference for reservoir dams as nesting sites. This range expansion, which started in the mid-1960s, also includes the Piedmont regions of Virginia, South Carolina, and Georgia, and in southcentral Florida (summary in Grant and Quay 1977).

Platania and Clark (1981) discuss the 1960-80 range expansion of northern rough-winged swallows (*Stelgidopteryx ruficollis*) in the North Carolina Coastal Plain and mapped the known breeding distribution of the species in the state. They also reported nesting season records of bank swallows (*Riparia riparia*) from Roanoke Island, Dare County, but a colony apparently never formed there. Bank swallows have nested sporadically in North Carolina. Earlier records were available from 1926 to 1940 in Henderson County (Nicholson 1951, Pickens 1954). Snively (1978) reported a colony in Wilkes County that was present from 1977 to 1978. This was the first recent nesting record for the state, but the colony has since died out. Subsequently, Lee and Hendrickson (personal observations) found a nesting colony near

Linville in the Mountains of North Carolina in 1991. All North Carolina nest sites are in artificial banks made by large earth-moving equipment.

Thus, it appears that current land use practices have provided open foraging habitats, and various man-made structures and land modifications have provided suitable artificial nest sites, thus allowing various species of swallows to expand their breeding range in the Southeast.

CONCLUSIONS

Like other species of swallows, the tree swallow has expanded its range considerably since the late 1800s. Earliest records show the species to be a peripheral breeding species in the southeastern United States, and nesting records are sporadically distributed both geographically and temporally (Fig. 1). Range expansion appeared to be gradual through the 1960s and then explosive from the 1970s to the present as the birds populated the Piedmont of Maryland, Virginia, and portions of North Carolina (Fig. 2). The species expansion in the mountains, Mississippi basin, and Coastal Plain occurred at different rates. Overall the species has spread south over 600 km in this century with approximately 220 km (35%) of this expansion occurring in the last decade. Although various factors such as land clearing were obviously necessary for the range expansion to occur, the timing of these changes in land use does not appear to correspond directly with the expansion in range.

Although land clearing probably benefited all species of swallows nesting in the Southeast, the change of distribution is also related to availability of nesting sites. Thus, the northern rough-winged swallow, the species with the least demanding requirements for nesting sites, was the first to expand its range. Barn swallows followed, expanding into the Piedmont and Coastal Plain as wooden bridges were replaced with concrete ones. Cliff swallows have nested in North Carolina only since the 1960s, and their current distribution is discontinuous and dependent on the large reservoirs constructed in the latter part of this century. Tree swallows expanded their range with the re-introduction of beavers and after their adoption of nest boxes. The bank swallow, which has the most restricted distribution, relies on exposed banks that are sporadically distributed and often not continuously available because of erosion and invading plant communities.

ACKNOWLEDGMENTS—I thank various participants of the North Carolina Breeding Bird Atlas program administered by the North Carolina State Museum of Natural Sciences for participation in our field studies. Herb Hendrickson, Julie Angerman-Stewart, Eloise Potter, Maurice

Graves, John Gerwin, Mary Kay Clark, Phil Crutchfield, and Norma and Bill Siebenhiller each reported nesting tree swallows. C. S. Robbins and G. A. Hall reviewed the manuscript and maps and provided additional information.

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Accepted 30 July 1992

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by

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An Observation of Fea's Petrel, *Pterodroma feae*
(Procellariiformes: Procellariidae), Off the
Southeastern United States, With Comments on the Taxonomy
and Conservation of Soft-plumaged and Related Petrels
in the Atlantic Ocean

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ABSTRACT—The soft-plumaged petrel and related species (*Pterodroma* spp.) remain one of the most poorly known seabird taxa in the Atlantic Ocean, and there is cause for serious concern over the continued survival of two North Atlantic forms. Soft-plumaged petrels were formerly considered to be a single, albeit morphologically variable, complex of one species. However, taxonomists now generally consider the complex to contain at least three species including the nominate. We report a marine occurrence of a North Atlantic species, probably Fea's petrel *P. feae*, from the South Atlantic Bight off the coast of the southeastern United States. We describe morphological characteristics for separating the various forms and consider the recent at-sea sightings in relation to dispersal factors such as seasonal wind regimes and coassociation with other seabird species that regularly disperse to western sectors from eastern sectors in the North Atlantic Ocean.

Gadfly petrels in the genus *Pterodroma* are known to disperse widely over the world's oceans, often at considerable distances from their natal colonies (Bourne 1967). Soft-plumaged petrels, *P. mollis* (Gould), are medium-sized gadfly petrels breeding in the Atlantic Ocean, the southern Indian Ocean, and the South Pacific Ocean. Although widely distributed, the number of island colonies is limited, and relative-

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ly few at-sea observations of either soft-plumaged or related northern populations have been made away from their breeding areas (Collar and Stuart 1985). We report such a sighting from the waters off the southeastern United States and provide some field marks (see also Enticott 1991) that may be useful for differentiating forms within a difficult taxonomic complex formerly regarded as a single species (Bourne 1983a).

Sighting description—On 9 November 1984, two of us (J.C.H. and C.A.F.) observed an unusual gadfly petrel with other procellariiforms during a census of seabirds at the edge of the continental shelf off the Georgia coast. A mixed flock (30-40 individuals) of the black-capped petrel, *Pterodroma hasitata* (Kuhl), Cory's shearwater, *Calonectris diomedea* (Scopoli), greater shearwater, *Puffinus gravis* (O'Reilly), and Audubon's shearwater, *Puffinus lherminieri* Lesson, accompanied by pomarine jaegers, *Stercorarius pomarinus* (Temminck), and herring gulls *Larus argentatus* Pontoppidan, was seen feeding over a fish school near the western frontal boundary of the Gulf Stream at 31°39'N, 79°24'W. This was approximately 145 km due east of St. Catherine's Island, Georgia (depth 250 m, surface temperature 25.5°C). We initially noticed a gadfly petrel without a white nape or rump in the feeding flock at 1625 EST. During the next 15 minutes, we watched from opposite ends of the stationary research vessel while the bird flew and foraged with other seabirds. It was seen from as close as 30 m through 9 x 35 and 10 x 40 binoculars.

J. C. Haney noted that, compared with the high bounding flight of nearby black-capped petrels, this gadfly petrel had more rapid wingbeats and flew closer to the ocean surface. It was not noticeably different in size from the black-capped petrel, and like that species, it alternated banking and gliding with first the dorsal and then the ventral surface exposed to the observers. The bird's overall appearance was dark gray above and white below. The gray tail was wedge-shaped and slightly paler than the back, without light-colored upper tail coverts. The crown appeared darker than the nape and hindneck, and the forehead was white. No dark facial mask around the eye was observed. There was conspicuous mottling or streaking along the bird's flanks. This field mark was very obvious and set the bird apart from nearby black-capped petrels which have clear white flanks. The bird did not have a complete breast band, although it did have a short, ventrally-projecting light gray bar on both sides of the neck in front of the wings. C. A. Faanes noticed that the underwing coverts were noticeably gray to the base of the primaries. The primary feathers appeared white-based, reminiscent of a jaeger in flight, suggesting that the bird may have been molting its wing coverts at the time. The upperwings

were medium gray, darker on the wing coverts. The bill was dark gray or black.

Taxonomy and identification—Various field guides on board indicated that the bird must belong to one of the North Atlantic gadfly petrels closely related to the soft-plumaged petrel *P. mollis*. The wholly dark underwing eliminated all other *Pterodroma* that have been documented as occurring in the North Atlantic (i.e., *Pterodroma hasitata*, *P. cahow* [Nichols and Mowbray], *P. arminjoniana* [Giglioli and Salvadori]). The gray coloration, contrast between back and tail, dark bill, and wholly white underparts ruled out similar petrels from other oceans (i.e., *Lugensa brevirostris* Lesson, *Pterodroma incerta* Bonaparte, *Procellaria cinerea* Gmelin). The soft-plumaged petrels, formerly treated as four or more subspecies (e.g., Mathews 1934, Harrison 1983), have recently been reclassified as three distinct species, *Pterodroma madeira* Mathews, *P. feae* (Salvadori), and the nominate *P. mollis* (Bourne 1983a, Imber 1985, Zino and Zino 1986; see also Sibley and Ahlquist 1990, Warham 1990). All three forms may appear to have various shades of dark gray-brown above, depending upon feather wear and lighting conditions (Enticott 1991). The nominate soft-plumaged petrels from the southern hemisphere are normally darkest, with variable gray markings extending across the upper breast and shading into the white face and chin above but contrasting sharply with the white belly below (Fig. 1). Thus, these birds appear to have a dark head and neck but pale face contrasting with white underparts. Some southern soft-plumaged petrels have a prominent "W" mark on the wing, some have noticeably paler rumps, and in some, the underwing shows variable amounts of contrasting white coloration. The North Atlantic forms are known as the Freira petrel (*P. madeira*) and Fea's petrel (*P. feae*; see Bannerman and Bannerman 1966; known also as "gon-gon" petrel on the Cape Verde Islands [Bourne 1983a, Collar and Stuart 1985]). These two species are both normally paler and grayer above than the nominate, with the entire body white below (Fig. 2, personal observation, J. Enticott personal communication). The amount of black around the eye in these forms ranges from conspicuous to essentially lacking. In general, photographs we examined indicated that both the underwings and upperwings are more uniformly colored in the North Atlantic species.

The Freira petrel and Fea's petrel are difficult to separate on the basis of plumage alone (Bourne 1983a, Fisher 1989). Fea's petrel is larger and is known to nest (in winter) only on the Cape Verde Islands and on Bugio (in the Desertas group), although there are recent sight and vocalization records from the Azores (Bibby and del Nevo 1991) and from Great Salvage Island 300 km south of the

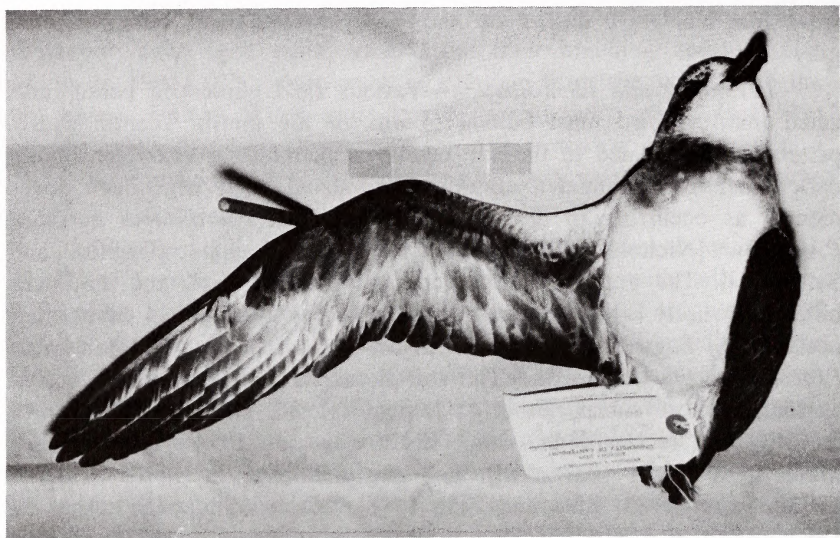


Fig. 1. Specimen of nominate *Pterodroma mollis*, showing underparts, collected from Antipodes Island, 13 February 1969, by J. Warham (Department of Zoology, University of Canterbury, Christchurch 1, New Zealand).

Madeiras (James and Robertson 1985). Measurements of wing and body length in Fea's petrel overlap extensively with the black-capped petrel (Cramp and Simmons 1977, Harrison 1983). When we (J.C.H. and C.A.F.) compared specimens of *P. feae* and *P. hasitata*, we concluded that size differences between these two species would be difficult to detect under field conditions. The Freira petrel (a summer breeder) is significantly smaller than either the Fea's petrel or the soft-plumaged petrel (Cramp and Simmons 1977, Fisher 1989). Bourne (1983a) stated the *P. madeira* has less mottling on the flanks than *P. feae*. However, other accounts differ (see Cramp and Simmons 1977, Harrison 1983), and such relative field marks may not be useful at sea in the absence of direct comparison and experience.

Status and distribution—We believe that the bird we observed must have been *P. feae* for the following reasons. First, the lack of a complete breast band eliminated southern soft-plumaged petrels. None of >290 specimens of the northern forms or numerous living examples examined by P. and F. Zino (personal communication) have a marked breast band, although a small minority of individuals with breast bands have been reported at sea off Madeira (taxonomic identity unknown; B. Zonfrillo personal communication). Generally, there is at least 1 cm of white between the two sides of the partial breast band in the northern species (F. Zino personal communication). Second, the large



Fig. 2. Photograph of *Pterodroma madeira*, showing distinctive dark underwing and pure white underparts, Madeira, 16 June 1969, P. A. Zino (Quinta da Vista Alegre, Rua do Dr. Pita 5, 9000 Funchal, Madeira).

size of the bird we observed (near or identical to black-capped petrel) indicates the Fea's petrel. Third, the population of the smaller Freira petrel is apparently reduced to only a few dozen pairs (A. and F. Zino personal communication), and it has not been recorded conclusively away from the breeding sites. Therefore, it seems less likely to be seen at sea. Finally, the Fea's petrel has been found wandering a similar distance before, e.g. to Israel where it was collected on 8 February 1963 (Bourne 1983b), although the majority of pelagic records for this form have been near the Canary Islands and off western Africa (Bourne and Dixon 1973, 1975; Lee 1984).

Neither the soft-plumaged nor related petrels have yet been accepted onto the official list of North American birds (cf. A.O.U. 1983, 1985). Lee's (1984) observation of a soft-plumaged petrel off North Carolina on 3 June 1981 was the first report for this continent; that individual had a complete breast band, a trait that points to a southern origin. It is notable that Lee's observation occurred during austral winter, a period when the southeast trade winds extend north across the equator and are liable to drift southern-hemisphere seabirds to the northwest Atlantic (comparable seasonal patterns for northward dispersal by seabirds occur in the Indian Ocean, see Ash [1983]). Similarly, the more northern Fea's petrel appeared off North America to the west of its breeding sites at a time when the northeast tradewinds still extend north. This pattern starts to deteriorate early in the northern winter after which time the westerlies move south to replace the northeast trades (at a time when the Fea's petrel was recorded as vagrant to Israel). In addition to our and Lee's (1984) records of soft-plumaged-type petrels off eastern North America, additional sight reports, including photographs of the nominate soft-plummed petrel, were made during May 1992, also off North Carolina (D. S. Lee personal communication, Anon. 1992).

DISCUSSION

We are aware of the inherent uncertainty in sight records of pelagic seabirds, especially *Pterodroma*, and we advocate photographic documentation when possible. However, we disagree with recent suggestions (Legrand 1985) that records of rare gadfly petrels off the eastern United States be supported with voucher specimens. Most countries, including the United States, have little jurisdiction over and limited protection for rare pelagic birds beyond coastal waters. Standard collection practices could further reduce the numbers of Atlantic petrels, some of which are now composed of only a few dozen breeding pairs. This risk seems unwarranted.

The soft-plumaged petrel complex remains one of the least known and seriously threatened seabird taxa in the Atlantic Ocean. There is cause for serious concern over the continued survival of the North Atlantic species. The total population of Freira petrels (*P. madeira*) may consist of no more than 50 pairs nesting at the higher elevations of Madeira, making it Europe's rarest bird (Buckle and Zino 1989). During the late 1980s, several failed breeding attempts were recorded, possibly because of interference by rats and/or predation by feral cats (A. Zino personal communication). The population of Fea's petrels (*P. feae*), which is unlikely to total more than several hundred pairs, is subject to human predation arising from medicinal use of the bird's body fat (Cramp and Simmons 1977, Collar and Stuart 1985). Breeding in dispersed colonies in burrows, earth screes, and rocky outcrops, this ground-nesting species is also vulnerable to predation by cats, rats, and other feral mammals; deforestation, vegetation destruction, and soil erosion by goats; and possible competition with rabbits for nesting burrows (Collar and Stuart 1985:42).

As in several other eastern and southern Atlantic procellariiforms (for examples, see Lee 1979, 1984; Haney and Wainright 1985), dispersal into the western Atlantic Ocean by petrels of the soft-plumaged complex could prove to be a regular occurrence overlooked owing to the species' rarity rather than casual vagrancy. Fea's petrels have been observed accompanying groups of Cory's shearwaters in the eastern Atlantic at other seasons (Lambert 1980). The mixed-species flock in which we encountered the Fea's petrel was dominated by Cory's shearwaters, a far more common species that occupies a sympatric breeding range with Fea's petrel in the eastern North Atlantic. If such interspecific associations are typical, then the petrel we observed may have followed, or have been locally attracted to, large flocks of trans-Atlantic migrant shearwaters during its wanderings to the offshore waters of the southeastern United States.

ACKNOWLEDGMENTS—We thank M. Lecroy of the American Museum of Natural History for the loan of specimens of *P. feae*, and E. McGhee of the University of Georgia Museum of Natural History for curatorial assistance. J. Warham, P. Meeth, B. Zonfrillo, S. M. Lister, and F. and P. A. Zino supplied additional information, including reference photographs of soft-plumaged and related petrels for comparison. We also thank D. H. White, F. Zino, and three anonymous reviewers for valuable comments on earlier drafts. The University of Georgia Marine Extension Service and crew of the R/V "Bulldog" extended logistic support during our offshore surveys. Additional support was received from The Pew Charitable Trusts under

the Marine Policy Center's program "Changing Global Processes and Ocean Conservation" at Woods Hole Oceanographic Institution (WHOI). This is WHOI Contribution No. 7763.

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Accepted 17 March 1992

ENDANGERED, THREATENED, AND
RARE FAUNA OF NORTH CAROLINA
PART I. A RE-EVALUATION OF THE MAMMALS

Edited by Mary Kay Clark

This book is a report prepared by a committee appointed in 1985 by the North Carolina State Museum of Natural Sciences to re-evaluate the list of mammals presented in *Endangered and Threatened Plants and Animals of North Carolina* (John E. Cooper, Sarah S. Robinson, and John B. Funderburg, editors. N.C. State Mus. Nat. Hist., Raleigh, 1977), which is now out of print. Committee members were Mary Kay Clark, David A. Adams, William F. Adams, Carl W. Betsill, John B. Funderburg, Roger A. Powell, Wm. David Webster, and Peter D. Weigl. The report treats 21 species listed in the following status categories: Endangered (5), Threatened (1), Vulnerable (6), and Undetermined (9). Most species accounts discuss the animal's physical characteristics, range, habitat, life history and ecology, special significance, and status (including the rationale for the evaluation and recommendations for protection) and provide a range map and an illustration of the animal's external characters. Ruth Brunstetter and Renaldo Kuhler illustrated the book. An introductory section contributed by Ms. Clark discusses the changes in status that occurred in the decade between 1975 and 1985. It also mentions efforts to protect marine mammals and includes a checklist of the cetaceans known from North Carolina.

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Cotton Mice, *Peromyscus gossypinus* LeConte
(Rodentia: Cricetidae), in the Great Dismal Swamp
and Surrounding Areas

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ABSTRACT—Livetrapping of small mammals was conducted in the Great Dismal Swamp and other areas of North Carolina in 1990. Five *Peromyscus gossypinus* were caught in the Dismal Swamp proper, and 42 were caught in the Chowan Swamp adjacent to the Dismal Swamp. These are the first published records of *P. gossypinus* taken in the Dismal Swamp region since the 1930s.

Rose et al. (1990) suggested that the cotton mouse, *Peromyscus gossypinus* LeConte, could be extinct in the Great Dismal Swamp of Virginia and North Carolina. With the exception of two specimens collected in 1933 by Dice (1940), virtually none has been captured there since the turn of the century despite the efforts of Handley (1979) in the 1950s and Rose et al. (1990) in the 1980s. Our recent collections and genetic analyses show *P. gossypinus* exists in the Dismal Swamp, and that based on capture rate it is uncommon in the Swamp proper, but is relatively abundant in areas adjacent to the southern section of the Swamp.

Separating *P. gossypinus* from *P. leucopus* Rafinesque (white-footed mouse) can be difficult both for live and museum specimens. Dice (1940) states that in eastern Virginia size characteristics but not color can be used to separate these species. Our studies (unpublished data) show that several cranial and external characters from adult specimens are required for consistent species identification with discriminant analysis. However, a fixed allozyme difference at the Glucose-6-Phosphate Isomerase locus (GPI or PGI, Enzyme Commission No. 5.3.1.9), and nearly fixed differences at the Albumin and alpha-Glycerolphosphate dehydrogenase (a-GPD or GPD), Enzyme Commission No. 1.1.1.8) loci separate these two species (Price and Kennedy 1980; Robbins et al. 1985; Boone 1990; Boone unpublished data).

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METHODS

We captured small mammals with Sherman livetraps in north-eastern North Carolina for studies examining subspecific affinities, population genetics, and Lyme disease (Magnarelli et al. 1992) in *P. gossypinus*. On 26 and 27 April 1990, we trapped in the Dismal Swamp along Highway 158 from 6.3 to 10.6 km east of Highway 32 (east of Sunbury, Gates County, North Carolina) for 587 trapnights. On 13 June 1990, we placed 200 traps in the Chowan Swamp between 2.9 and 5.3 km south of Gatesville (Gates County, North Carolina). On 28 and 29 April 1990, we trapped along the Cashie River in and around Windsor (Bertie County, North Carolina) for 350 trapnights, and we placed 150 traps in and around Richlands (Onslow County, North Carolina) on 30 April 1990.

Locations of trap lines and specific traps were selected to maximize the capture of *P. gossypinus* based on our understanding of its habitat preference and ecology learned from the capture of more than 2,100 cotton mice from throughout its entire range. Although these mice can be caught almost anywhere, they seem to exist in highest densities in thick, undisturbed (anthropogenic or natural), seasonally flooded, riparian woodlands near water. On coastal barrier islands where these habitats do not exist, they seem to occur most densely in undisturbed old-growth oak-palmetto (*Quercus* sp. and *Serenoa repens*) forests. Traps were set on, in, and under logs, in trees, under stumps, in the rotten bases of trees, on the edges of ponds, on floating debris in flooded forests, as well as in old buildings and trash piles. More than one trap was set in particularly promising sites.

We used allozyme markers to identify the *Peromyscus*. Genetic analysis was performed with standard horizontal starch gel electrophoretic and protein staining techniques on blood, liver, and muscle for 42 enzyme and protein loci. Techniques were similar to those of Selander et al. (1971) as described in Boone (1990).

Body mass was measured to the nearest 0.1 g. Age (juvenile, subadult, or adult) was determined by pelage color, and reproductive status was determined by examination of external and internal reproductive structures. Non-adult and pregnant females were deleted from morphological comparisons.

RESULTS

Peromyscus gossypinus was captured in each of the four areas examined, and *P. leucopus* was captured in all areas except Richlands (Table 1). Additionally, one golden mouse (*Ochrotomys nuttalli* Harlin) and one juvenile Virginia opossum (*Didelphis virginiana*

Table 1. *Peromyscus gossypinus* and *P. leucopus* captured in North Carolina, 1990.

Location	Species			
	<i>P. gossypinus</i>		<i>P. leucopus</i>	
	Number caught	Captures/ 1,000 trapnights	Number caught	Captures/ 1,000 trapnights
Gates County Dismal Swamp	5	8.5	27	46.0
Gates County Chowan Swamp	42	210.0	2	10.0
Bertie County Windsor	33	94.3	5	14.3
Onslow County Richlands	42	280.0	0	0.0

Kerr) were captured in the Dismal Swamp, and one *Blarina* was captured at Windsor.

We found that Dice's (1940) suggestion that these *Peromyscus* species can be distinguished by size is not strictly true. Our comparison of genetic markers and morphology indicates that although *P. gossypinus* tends to be larger and heavier than *P. leucopus*, there is considerable overlap. For the mice caught east of Sunbury, body mass of *P. gossypinus* ranged from 20.9 to 35.5 g (\bar{x} = 26.3 g, n = 5), whereas *P. leucopus* ranged from 14.6 to 24.6 g (\bar{x} = 19.1 g, n = 26). In the Chowan Swamp, body mass of *P. gossypinus* ranged from 17.1 to 36.8 g, (\bar{x} = 25.9 g, n = 42); the one adult *P. leucopus* weighed 15.9 g. In the Windsor area, *P. gossypinus* ranged from 19.2 to 37.9 g (\bar{x} = 28.4 g, n = 22), and *P. leucopus* ranged from 17.1 to 24.1 g (\bar{x} = 20.4 g, n = 4). The *P. gossypinus* from Richlands ranged from 21.2 to 39.4 g (\bar{x} = 29.2 g, n = 33). Therefore, if Rose et al. (1990) used size to identify *Peromyscus*, some of the specimens identified as *P. leucopus* by might actually have been *P. gossypinus*.

DISCUSSION

Our results probably differ those of Rose et al. (1990) as a result of different trapping location, design, and methods. In the southern portion of the Dismal Swamp, Rose et al. (1990) used pitfall traps set on a grid. We used only Sherman live-traps, and our collection locations were selected to target habitats thought to be optional for *P. gossypinus* without concern for determining density or other demographic parameters. Therefore, we were not confined to a grid, and we were able to trap in areas, and place traps in sites, that would be inappropriate to use with pitfall traps in a demographic study. Furthermore, our trapping was only conducted in the southernmost part of

the Swamp, an area more accessible to migrants from the Chowan Swamp where *P. gossypinus* is abundant, whereas the majority of Rose et al.'s (1990) effort was concentrated in the northern section of the Swamp where *P. gossypinus* might be absent.

Although *P. gossypinus* is abundant in areas near the Dismal Swamp, it is probably not currently abundant in the swamp proper. Handley (1979) stated that *P. gossypinus* densities fluctuate widely in the Swamp, and this population could simply be at a low point in its cycle. This species now occurs in the Great Dismal Swamp, but current management practices in the Great Dismal Swamp National Wildlife Refuge that promote clearings and vegetational heterogeneity might endanger it because we have observed that *P. gossypinus* occurs in greatest density in mature, undisturbed riparian forests.

ACKNOWLEDGMENTS—The Savannah River Ecology Laboratory under contract DE-AC09-76SR00819 between the U. S. Department of Energy and the University of Georgia's Institute of Ecology, the University of Georgia Museum of Natural History, Sigma Xi, and the Theodore Roosevelt Memorial Fund administered by the American Museum of Natural History provided support for this work, and Kevin Roe assisted with the trapping.

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Accepted 1 September 1992

ENDANGERED, THREATENED, AND
RARE FAUNA OF NORTH CAROLINA
PART II. A RE-EVALUATION OF THE MARINE
AND ESTUARINE FISHES

by

Steve W. Ross, Fred C. Rohde, and David G. Lindquist

This is the second in a series of reports by committees appointed in 1985 by the North Carolina State Museum of Natural Sciences to re-evaluate the faunal lists presented in *Endangered and Threatened Plants and Animals of North Carolina* (John E. Cooper, Sarah S. Robinson, and John B. Funderburg, editors. N.C. State Mus. Nat. Hist., Raleigh, 1977), which is now out of print. The report on marine and estuarine fishes by Ross, Rohde, and Linquist treats one Endangered species, six Vulnerable species, and four anadromous fishes that, while not formally listed, are of some concern. Five species listed as being of Special Concern in 1977 no longer warrant formal status. The publication includes six original drawings by Renaldo Kuhler.

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Observations Regarding the Diet of Florida Mice, *Podomys floridanus* (Rodentia: Muridae)

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ABSTRACT—The diet and feeding behavior of the Florida mouse (*Podomys floridanus*) were examined during an ecological study in Putnam County, Florida. Field and laboratory observations provided additional evidence that *Podomys* takes a wide variety of plant and animal foods. Preliminary preference tests with acorns from six species of oaks suggest that acorns of the dominant species (*Quercus laevis*) in the study area are less favored than those of other species. The crash of a population where supplemental food was provided suggests that local populations are not food limited.

Almost nothing is known about the natural diet of the Florida mouse, *Podomys floridanus* (Chapman). Merriam (1890:53) reported an observation that these mice ate seeds of "scrub-palmettoes" in southeast Florida. The association of *Podomys* with turkey oaks (*Quercus laevis*) and other oaks was noted by Merriam (1890) and Bangs (1898); Layne (1970), Humphrey et al. (1985), and Packer and Layne (1991) suggested that acorns were a major food during mast years. Milstrey (1987) described *Podomys* eating engorged soft ticks (*Ornithodoros turicata americanus*) that parasitize gopher frogs (*Rana capito*) and gopher tortoises (*Gopherus polyphemus*). Presumably other foods include insects, seeds, nuts, fungi, and other plant material (Layne 1978, Jones and Layne In Press). The study by Packer and Layne (1991) is the first to examine foraging behavior of this species.

Effects of food supplies on local distributions of *Podomys* also have been poorly studied. The only attempt to determine whether populations are limited by food availability was the supplementation experiment performed by Young (Young 1983, Young and Stout 1986) on two grids in sand pine (*Pinus clausa*) scrub in Orange County, Florida. Other rodents responded to the additional food, but *Podomys* rarely appeared on grids and failed to establish a permanent population during the experiment, although the species was abundant previously. Young (1983) concluded that *Podomys* populations were limited by factors other than food.

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The purpose of this article is to report observations of feeding behavior of wild and captive *Podomys*. Additionally, I performed acorn preference tests and a supplemental feeding experiment to determine whether local distributions were due to food supply.

MATERIALS AND METHODS

Field Studies—Florida mice were trapped on the Anderson-Cue and Smith Lake sandhills on the Katharine Ordway Preserve-Swisher Memorial Sanctuary in Putnam County, Florida. These xeric sandhills are "high pine" communities dominated by longleaf pine (*Pinus palustris*) and turkey oak (*Q. laevis*). Brand (1987), Eisenberg (1988), Franz (1986, 1990), and Jones (1990) described the fauna of these sandhills. Populations of *Podomys* occur on sandhills and old pastures on the Ordway Preserve, where they are closely associated with burrows of gopher tortoises. Cotton mice (*Peromyscus gossypinus*) and golden mice (*Ochrotomys nuttalli*) inhabit lower, more mesic habitats on the preserve.

Each tortoise burrow on the Anderson-Cue and Smith Lake sandhills was flagged and marked with a unique number. Florida mice were caught in Sherman traps placed at the mouths of tortoise burrows on both sandhills. Animals were released near the burrow entrance so that I could observe escape responses and foraging behavior (Jones 1990). I used standard mark-and-recapture techniques, in which individuals were toe-clipped, sexed, and weighed. I calculated minimum trappability $[(\text{number of captures} - 2)/(\text{possible captures} - 2)]$ for animals captured three or more times (Hilborn et al. 1976).

I used a breeding colony derived from animals captured at Ashley Old Pasture and near Smith Lake to perform food preference tests. Captive animals were housed in aquaria fitted with hardware-cloth tops. The maintenance diet consisted of rodent chow (Wayne Rodent Blox) and water provided ad libitum, supplemented with lettuce, carrots, apples, strawberries, sunflower seeds, mixed bird seed, oatmeal, mealworms, and crickets.

Preference Tests—I performed preference tests to determine whether acorns of turkey oaks (*Q. laevis*) were selected over acorns of other species present on the Ordway Preserve. At least 24 hours before beginning a test, a mouse was placed in an aquarium with clean kitty litter, nesting material, water, and rat chow. To start a trial I removed the chow and added three bowls, each containing five acorns of a single species, at about 1900 hours. Each acorn was marked, weighed, and measured, but no effort was made to ensure that all acorns in a bowl were identical in size. I controlled for location effects by shifting relative positions of the three types of acorns in

each trail. Acorns with weevil holes were not used, and in a single trial all acorns either had caps or lacked them. Approximately 12 hours later I removed bowls, acorns, and acorn fragments. I recorded whether acorns were removed from bowls and whether they were opened and eaten, opened and evidently not eaten, gnawed, or apparently untouched. After discovering that some acorns lacking external holes were spoiled by insects or mold, I simplified analysis of results by recording only whether acorns were opened, regardless of whether any meat appeared to have been removed. Ranked data were subjected to the Friedman test (Conover 1980) to test the null hypothesis that species of acorns were opened in equal numbers.

Food Supplementation—The food supplementation experiment consisted of trapping at three grids, two on Anderson-Cue (designated ACI and ACII) and one on Smith Lake (SL). Each grid consisted of 10 columns and 10 rows 10-m apart, with a single Sherman trap at each intersection (area = 10,000 m²). Prior trapping at burrows in each area indicated that mice were present, and grids were set more than 100-m apart to reduce movements of animals between grids. In April, May, and June, 1987, I trapped SL for 800 trapnights and determined that after three consecutive nights of trapping, no additional individuals were captured. Consequently, SL, ACI, and ACII were trapped for three consecutive nights per month for a total of 300 trapnights/grid monthly. On ACI I provided a mixture of sunflower seeds, mixed bird seed, and oatmeal for 1 year in seven chick feeders fitted with glass jars. To eliminate non-target species, plastic buckets with two holes (2.5 cm) cut near the rims were upended over the feeders and anchored with cinder blocks.

RESULTS

General Observations on Diet—Five feeding events were observed at Smith Lake. An adult male caught and released on SL (5 May 1988) readily ate a cricket (*Orthoptera: Gryllinae*) offered to him. On 15 June 1987 at approximately 0245 EST, an adult female (who had been trapped and released) immediately caught a small moth and consumed all but the wings. On 9 May, an adult female just released from a trap ate a young shoot of wild bamboo (*Smilax auriculata*). In July 1988, a female released from a trap at a burrow hid in a hole at the base of a turkey oak approximately 5 m northwest of the burrow. In a few minutes she left the hole, picked up a small pawpaw (*Asimina incarna*), carried it back to the hole, and ate it. Jones (1989) previously described consumption of a pawpaw fruit (*A. incarna*) by a Florida mouse at Smith Lake. Predation and dispersal of *Asimina* fruits have not been well studied, although

these fruits are eaten by opossums (*Didelphis virginiana*), humans, and other mammals (Bartram 1791, Willson and Schemske 1980, Norman and Clayton 1986). Although nutritional values and fruit set have not been reported for *A. incarna*, it is the most abundant pawpaw and the largest fruit produced in sandhills on Ordway and probably represents a significant addition to the summer diet of *Podomys*.

I offered captive animals the following fruits and seeds collected at Ordway, all of which were eaten: acorns (*Q. chapmanii*, *Q. geminata*, *Q. hemisphaerica*, *Q. laevis*, *Q. myrtifolia*, and *Q. nigra*), pine seeds (*P. elliotii* and *P. palustris*), blueberries (*Vaccinium myrsinites*), deerberries (*V. stamineum*), gall berries (*Ilex galabra*), blackberries (*Rubus argutus*), gopher apples (*Licania michauxii*), pawpaw fruits (*A. incarna* and *A. pygmaea*), flowers of queen's delight (*Stillingia sylvatica*), and seed pods of legumes (*Crotalaria rotundifolia* and *Galactia elliotii*). Captive mice also shredded seeds and stems of unidentified grasses and incorporated them into the cotton nesting material in their cages; the grasses probably were eaten as well.

The ready acceptance of a wide variety of foods in my study implies that, like *Peromyscus*, *P. floridanus* is an opportunistic feeder. In general, the feeding behavior I observed in captive *P. floridanus* resembled that described for *Peromyscus* (Eisenberg 1968), in which the animal picks up food with the paws or mouth, then crouches and manipulates the food with the paws. Large items such as pawpaws were propped against the substrate. Seed pods were opened by grasping the pod vertically, resting one end on the substrate, chewing off one end, and opening the pod longitudinally along a suture. Larger foods, such as turkey oak acorns, were dragged with the incisors; smaller items were carried in the mouth. Some captives consistently cached acorns and sunflower seeds under kitty litter in corners of the aquaria. Food items and remains also commonly were found underneath nests.

Except for smaller acorns that might be split in half, acorns were opened consistently at the hilum (basal scar). Although acorns typically were carried by the point at the distal end, mice never chewed open the hull there. For small, round acorns a neat incision was made around the hilum; on more elongate nuts (*Q. geminata* and *Q. laevis*) the hull was nibbled farther down the sides. Caps, if present, were removed; there was no significant difference in the numbers of capped and capless *Q. laevis* acorns opened.

Predation on vertebrates is probably rare. On Smith Lake in 1983, J. F. Eisenberg (University of Florida, personal observation) trapped an adult male who detached and ate the posterior part (about

3.5 cm) of a juvenile red snake (*Elaphe guttata*) that was caught half way in the trap. An adult male caught on Anderson-Cue in October 1987 ate the viscera of a juvenile Florida mouse also caught in the trap. A litter of three young was eaten on one occasion when a male and two lactating females were in one aquarium.

Acorn Preferences—Unpredictable acorn supplies made it impossible to run tests with identical acorns in 1988 and 1989. Additionally, the majority of acorns on the ground already contained weevil larvae or were otherwise spoiled. In 1988, I concentrated on determining which acorns were eaten by *Podomys*. I presented acorns from six species of oaks—Chapman's (*Q. chapmanii*), live (*Q. geminata*), turkey (*Q. laevis*), laurel (*Q. hemisphaerica*), myrtle (*Q. myrtifolia*), and water oaks (*Q. nigra*)—to four captive animals. Five of these species belong to the red oak group, which generally contains three or four times more tannin (Briggs and Smith 1989) than species of the white oak group (which includes *Q. chapmanii*). Each mouse was presented with turkey oak acorns in combination with acorns from two other species; two–four trials were run per animal for a total of 12 trials. Although the sample was inadequate for statistical analysis, I noted that mice opened acorns of all species, and in all but one trial turkey oak acorns were opened in the smallest numbers.

In 1989 Chapman's and live oak acorns were not available, so I gathered acorns from *Q. laevis* and two different trees of *Q. hemisphaerica*, one from an old pasture near Ross Lake and the second from a hammock past Anderson-Cue. I expected that acorns of *Q. laevis*, the predominant oak on Smith Lake, would be preferred. I tested nine animals, two trials each. I analyzed the results of the first trial only, because there was no difference in ranks of first and second trials. Results indicated that acorns were not opened in equal numbers (Friedman test, $T = 26.75$, $P = 0.01$). For multiple comparisons at a significance level of $P = 0.01$ (Conover 1980), acorns from Ross Lake (*Q. hemisphaerica*) were opened significantly more often; differences between acorns from the hammock and from *Q. laevis* were not significant. These results indicate not only a preference for laurel oak acorns, but an ability to distinguish acorns from two individuals of *Q. hemisphaerica*.

Mice did not eat blackened nutmeats, but I did not test preferences of sound acorns versus acorns with larvae. On one occasion an adult female immediately ate a larva from an acorn opened but not eaten by another female. Semel and Andersen (1988) suggested that such differences in behavior might be due to mice being unable to detect larvae in unopened acorns, or that larvae are detected but avoided by some individuals. They also suggested that tooth marks

on hulls and movement of acorns might represent assessment. Of the 450 acorns presented in 30 trials to 13 *Podomys*, 66% were removed from bowls, whether opened or not.

Food Supplementation Experiment—Individual trappability of Florida mice captured on the Ordway Preserve ranged from 14 to 100% (Jones 1990). The average trappability for 5 years of trapping was 57%. According to Hilborn et al. (1976), estimates of minimum numbers of individuals by direct enumeration become more reliable as trappability exceeds 50%.

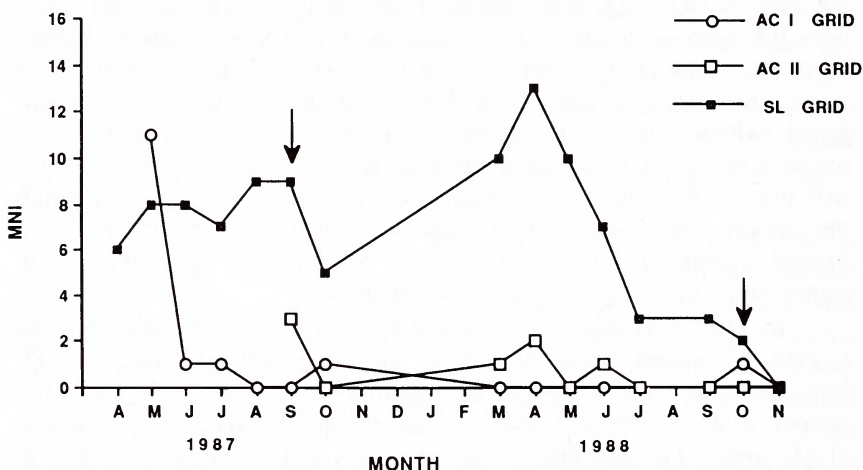


Fig. 1. Minimum number of individuals known alive (MNI) on the Anderson-Cue I, Anderson-Cue II, and Smith Lake grids in Putnam County, Florida. Arrows indicate beginning and ending of food supplementation on Anderson-Cue I.

Results of the food supplementation (Fig. 1) were similar to those reported by Young (1983) in that *Podomys* disappeared during the summer in spite of the additional food. Capture rates declined sharply on ACI where extra food was provided, although mice persisted in small numbers at burrows west and east of the grid. Maximum trapping success for a single night was 9%, and was usually much lower. Persistence (time between first and last captures) of mice on the three grids was estimated (Table 1). It seems unlikely that the decline on ACI was due to competition with immigrating rodents; the only other rodents captured on these grids were flying squirrels (*Glaucomys volans*).

Table 1. Persistence data for *Podomys* on trap grids in Putnam County, 1987-88. Data presented are minimum number known alive, mean + SD days present on grid, and total number of trapnights.

Grid Location	Number of Days Present				Trapnights
	Minimum Number	\bar{x}	SD	Maximum	
Anderson-Cue I	12	16	21	75	4,200
Anderson-Cue II	6	7	13	33	3,000
Smith Lake	24	123	156	517	4,100

DISCUSSION

Hulls of *Q. laevis* found in excavated burrows (Jones and Franz 1990) and vacuumed remains of *Q. geminata* and *Q. laevis* from burrows on Roberts Ranch, Putnam County (E. G. Milstrey, University of Florida, personal observation) were opened in a manner consistent with that observed with captive *Podomys*. Small piles of similarly-opened hulls occasionally were found at the base of turkey oaks and near burrow entrances on Ordway.

Acorn selection might be based on chemical composition other than tannin content. Acorns of *Q. hemisphaerica* contain more tannic acid than *Q. laevis* and more fat and carbohydrates than *Q. chapmanii* and *Q. incana* (Halls 1977, Harris and Skoog 1980). In their study of acorn preference in *Peromyscus*, Briggs and Smith (1989) found that five *P. leucopus* captured in habitats lacking oaks consumed equal amounts of acorns from species of the red and white oak groups, whereas mice from areas containing oaks selected acorns of *Quercus* species found in their habitat, independent of fat, protein, and tannin content.

Based on these preliminary results, I suggest that acorns of oaks other than *Q. laevis* are preferred if available. Turkey oaks provide an unreliable food supply. Umber (1975) noted low, variable acorn production by *Q. laevis* in Citrus and Hernando counties, and Kantola and Humphrey (1990) found that production by trees at Ordway varied with slope and tree diameter. Layne (1990) correlated the relatively greater abundance of *Podomys* in scrub and scrubby flatwoods with higher and more consistent acorn production than in sandhills. He also presented evidence that differences in morphology and behavior in scrub and sandhill populations reflect differences in vegetation structure and mast production in these habitats. Proximity to *Q. geminata* and other oak species might partially explain the relatively higher and more stable population of *Podomys* at Smith Lake, although there is no evidence that populations are food limited.

If oak species in hammocks are more reliable producers, the distribution of *P. gossypinus* and *Ochrotomys nuttalli* in hammocks at Ordway might be partly due to the acorn supply. Competition could be one factor restricting *Peromyscus* to sandhills when other rodents are present in contiguous habitats. However, in sandhills and other habitats elsewhere in Florida, *P. floridanus*, *P. gossypinus*, and *O. nuttalli* are sympatric (Packer and Layne 1991, Frank and Layne 1992).

ACKNOWLEDGMENTS—I thank the Florida Game and Fresh Water Fish Commission for permits that allowed this work; the Florida Museum of Natural History for space for the captive colony; and J. F. Eisenberg, R. Franz, J. N. Layne, and an anonymous referee for comments on an earlier draft. J. F. Anderson, L. S. Fink, W. H. Kern, R. F. Labisky, C. A. Langtimm, P. Ryschkewitsch, and C. A. Woods also provided assistance. The original version of this paper appeared in a dissertation presented to the University of Florida.

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